SPECIES COMPOSITION, DISTRIBUTION, AND PHYTOSOCIOLOGY OF KALSOW PRAIRIE, A MESIC TALL-GRASS PRAIRIE IN IOWA

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Abstract.— Species composition, distribution, and phytosociology of an 8 hectare area of tall grass prairie was intensively studied. Elevation and soils data were correlated with species distribution patterns. All species showed a response. Nine general patterns of distribution were observed in relation to elevation and soil types. Ordination and interspecific association analyses were used to identify clusters or groups of species having similar ecological amplitudes. *Sporobolis heterolepis* is the dominant plant of the upland prairie. The vegetation of the prairie is best described and represented by the continuum concepts of phytosociology.

A government survey started in March 1832, when Iowa was still a territory, and completed in August 1859 first documented the original extent of Iowa's prairie. The survey indicated that in the 1850s grassland covered about 85 percent of Iowa (U.S. Government 1868, Hayden 1945, Hewes 1950, and Dick-Peddie 1955). Today there are only a few tracts of this once vast Iowa prairie remaining.

Provision for state-owned prairies was made in 1933 when the Iowa State Conservation Commission prepared a report known as the Iowa Twenty-five Year Conservation Plan. This plan led to the purchase of several prairies that are now owned by state agencies. The prairies were purchased and set aside as natural areas with the intent that the various typical landscapes, wild flowers, and wild life of the native tall-grass prairie region be preserved for posterity. It was also intended that these areas would be useful as game and wild life sanctuaries; as examples of the native prairie soil types, where comparisons could be made with cultivated soils of the same soil association; and as reserves of prairie where scientific investigations could be made on problems concerning the native vegetations, floras, and faunas of the various topographic, climatic, and prairie districts throughout Iowa. Therefore, they were meant to serve as a reference point by which future generations could compare the influences of man on Iowa since settlement (Hayden 1946, Moyer 1953, Aiiman 1959, Landers 1966).

Kalsow Prairie, 64.8 ha (160 acres) of unplowed grassland in Pocahontas County, Iowa, is one such area. Criteria for its purchase dictated that this area satisfy the requirements of a game preserve, contain one or more soil types of an association, and include several regional vegetation types (Hayden 1946). Since its purchase in 1949 it has been the object of several studies on the nature and description of its vegetation, soils, management, insects, response to fire, mammals, and nematodes (Moyer 1953, Ehrenreich 1957, Esau 1968, Richards 1969, Brennan 1969, Norton and Ponchillia 1968, Schmitt 1969).

The characteristics of Iowa prairie in terms of vegetation types, structure, and general ecology of the dominant species was the subject of several papers during the 1930s and 1940s (Steiger 1930, Rydberg 1931, Weaver and Fitzpatrick 1934, Hayden 1943). These authors recognized the existence of six major types of grassland or vegetative communities and generally concluded that water relations, as affected by climate, soil, and topography, are responsible for local variations in the structure and distribution of Iowa prairie vegetation. Weaver and Fitzpatrick (1934) state:

> In varying the water relations of soil and air they merely bring about changes in the groupings of the dominant grasses and accompanying segregations and rearrangements of the forbs.

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The major grassland types, as alluded to in the above studies, were labeled "Consociations" after Weaver and Clements (1938) and were designated as follows:

1. Big Bluestem type (*Andropogon gerardi*)—found on the lower moist slopes and well-aerated lowlands.
2. Slough Grass type (*Spartina pectinata*)—found on poorly aerated and wet soils of sloughs and natural drainage systems.
3. Tall Panic Grass-Wildrye type (*Panicum virgatum* and *Elymus canadensis*)—found to occur on soils intermediate between Slough Grass and Big Bluestem types.
4. Little Bluestem type (*Schizachyrium scoparius*)—most important upland type (well-drained soils).
5. Needle Grass type (*Stipa spartea*)—found on the uplands, often occurring as a narrow zone following the shoulders of the ridges.
6. Prairie Dropseed type (*Sporobolus heterolepis*)—found locally on the dryest upland sites.

Moyer (1953), Aikman and Thorne (1956), Ehrenreich (1957), and Kennedy (1969) in recent studies present ecological and taxonomic descriptions of four state-owned native prairie tracts. All accounts contain extensive reviews of prairie literature. The vegetation complex as treated in these studies is limited basically to upland prairie. The studies also include information on soils, microclimate, topography, and management. Aikman (1959) reviewed in some detail the state of prairie research in Iowa.

Investigations involving the distribution of individual species within the prairie association began with the work of Shimek (1911, 1915, 1925). Weaver (1930) and Weaver and Fitzpatrick (1932) discuss the role of the major grasses and forbs within the community. Steiger (1930) and Cain and Evans (1952) mapped the spatial distributions of several species. They conclude that the principal factors affecting the local distribution patterns of prairie species are as follows: (1) microclimatic conditions, (2) edaphic variations, (3) the biology of the species concerned, particularly methods of reproduction and dispersal, (4) the relations of the species and other organisms, animal as well as plant, occurring in the community, and (5) the element of chance in the dispersal and establishment of new individuals. Local distribution patterns of species have been of interest to many ecologists (Curtie 1955, Kenshaw 1964, Sanders 1969).

Species in general show varying degrees of aggregation or association due to exhibited preferences for or tolerances of certain environmental conditions. The distributional patterns and interactions of the component species of a community express its phytosociological structure. Studies of grassland phytosociology have been concerned with either classification or ordination of basic species groups (Crawford and Wishart 1968).

This investigation was undertaken to provide information on the phytosociology of an 8 ha tract of Kalsow prairie in relation to edaphic and topographic variation. It includes information on species composition and distribution, factors affecting the distributional patterns of these species, community types, and interrelationships within and between these communities.

MATERIALS AND METHODS

Study Site

Kalsow Prairie is one of several state-owned Iowa prairies. It is 5 miles northwest of Manson, Iowa, and comprises the NE ¼ of Section 36, Belleville Township, T 90N, R 32W, Pocahontas County. It occurs in a part of northcentral Iowa that was glaciated during the most recent advances of the Wisconsin Glacier and within the Clarion-Nicollet-Webster soil association area (Ruhe 1969). The area was chosen for study on the basis of its vegetational composition (i.e., floristic richness and the presence of several plant community types).

The Vegetation

Taxonomy

Voucher specimens from the prairie were collected in duplicate throughout the growing seasons. All specimens were identified, and identical sets have been deposited in the herbaria of Iowa State University, Ames, Iowa, and Brigham Young University, Provo, Utah. Nomenclature follows Pohl (1966) for the grasses, Gilly (1946) for the sedges, and Gleason (1952) for the forbs.

Community Types

The 8 ha tract within Kalsow Prairie is adjacent to the south boundary of Kalsow Prairie and contains within its borders two vegetation types or subcommunities. These vegetation units were identified and delimited as follows (Fig. 1):

1. Upland prairie—includes a major portion of the study area on the ridges and adjacent lower slopes.
2. Potholes and drainage—found in the swales and lowlands of the study site.

The vegetation of these community types was analyzed using two separate approaches. The first involved the identification and listing of all species found within their boundaries. The second utilized random plots to determine percent cover, composition, and

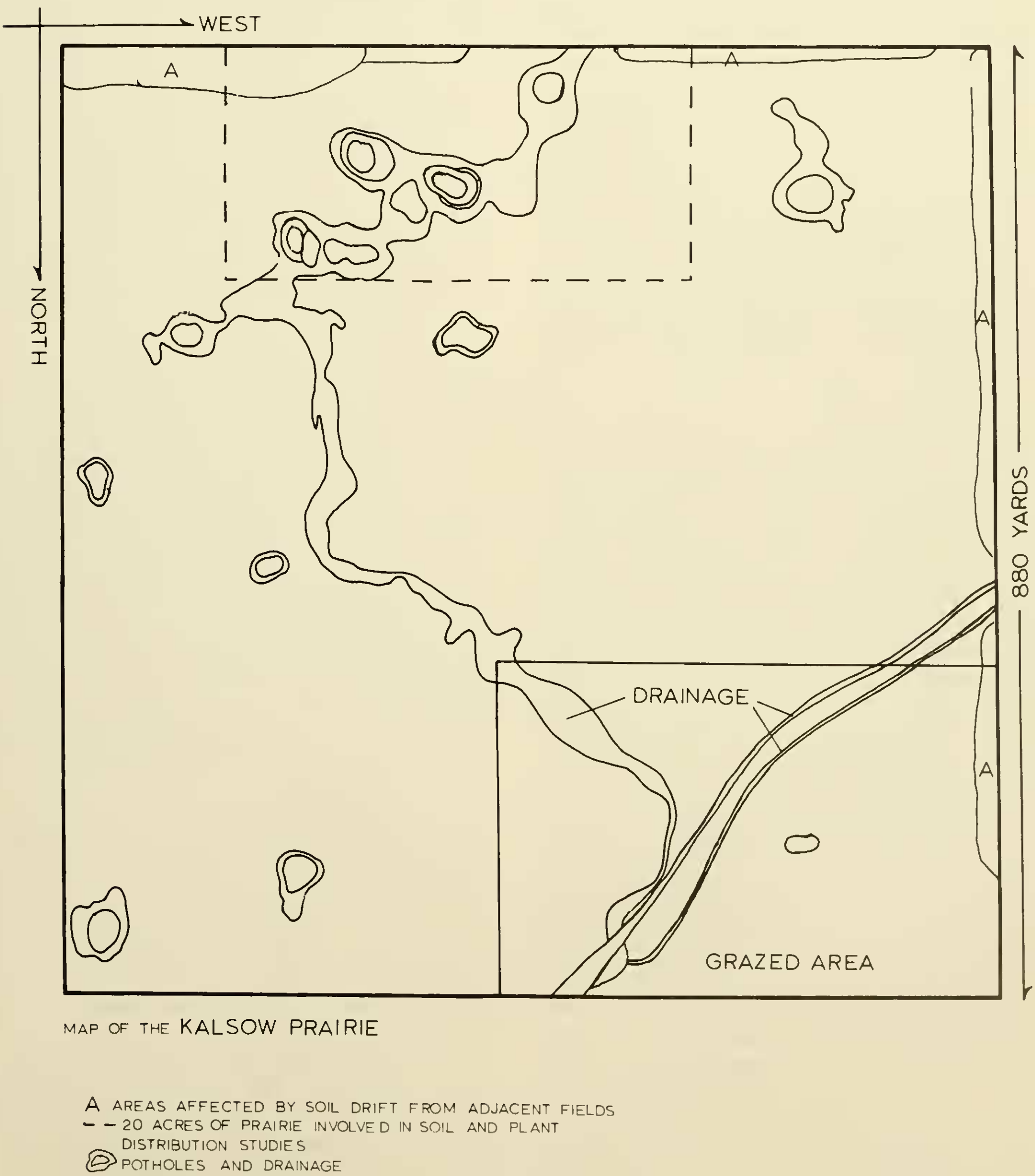

Fig. 1. Map of Kalsow Prairie.

interspecific relationships of species within these subcommunities.

Quadrat Analysis

The vegetation of each area was sampled by using 20 × 50 cm (1000 cm^2) quadrats. The quadrats were located on a restricted basis to reduce bias and to keep adjacent quadrats equal distances apart. Sampling was done between August 1 and September 15, when most species had reached their maximum growth. Cover estimates were made for each quadrat through use of Daubenmire's (1959) method.

Coverage was determined separately for all species overlapping the plot regardless of where the individuals were rooted. Coverage was projected to include the perimeter of overlap of each species regardless of superimposed canopies of other species. The canopies of different species are commonly interlaced or superimposed over the same area; therefore coverage percents often total greater than 100 percent.

Community Analysis

Plant distribution and topographic studies. An 8 ha (20 acres) plot of prairie (Figure 1) containing a large segment of potholes and drainage was selected and staked off in a 9 × 9 m grid. Each 27 square-meter block was then surveyed and a presence list compiled for all plant species found within the area. A total of 968 blocks was thus surveyed, and distribution data were tabulated for 160 species. Topographic readings were taken at 968 points and recorded in tenths of feet on the same 8 ha grid. Points were located at the corners of the 27 square meter plots.

Soil mapping. Soils were mapped on the 8 ha intensive study area. Mapping was done in cooperation with the Iowa State University Soils Survey under the supervision of Dr. Thomas E. Fenton, with Mr. J. Herbert Huddleston doing the actual mapping in the field. The mapping criteria for decisions on soil series delineation were as follows:

A Clarion—typical well-drained soil on convex ridges. Surface color 10YR 2/2–3/2; subsoil color 10YR 4'3–5'4.

A⁻ Clarion-Nicollet—an intergrade with respect to drainage as interpreted from the color profile. Surface is still 10YR 2/2–3/3, but the subsoil colors are duller, not exceeding /3 chroma. Profile is not mottled as in Nicollet.

N Nicollet—typical Nicollet, 10YR 2⅛–2/2 surface color, /2 chromas in the subsoil, which is mottled. Depth to carbonates generally greater than 30 inches.

Na Calcareous Nicollet—as above, but calcareous at some depth less than 30 inches.

W Webster—typical Webster with black (N2/–10YR 2/1) surface colors and gray (10YR 4/1–4/2–5/2) subsoil colors. Depth to gray subsoil ranges from 23/41 inches, but is commonly 30–35 inches. Carbonates occur at some depth below 22 inches, but the usual range in depth to carbonates is 22–36 inches. Some soils identified as Webster are noncalcareous in the entire probe depth (42 inches).

Wh Heavy Webster—typical colors of Webster but heavier textures, stronger development in the B and a lack of carbonates in 42 inches. In many places spots of Wh are included in the regular Webster mapping unit. On the other hand, some areas identified as regular Webster but noncalcareous to 36 inches or more might better have been called heavy Webster. The Webster soils, as mapped, include a rather broad range of texture and depths to carbonates, which could be more precisely subdivided only with further investigations.

N⁻ Webster-Nicollet—an intergrade whose surface color and friability is like Nicollet but whose subsoil is darker or grayer than true Nicollet. The soil is drier than Webster.

Na⁻ Calcareous Webster-Nicollet—as above but calcareous somewhere above 22 inches.

H Harps—typical Harps, a loamy, weakly developed soil that effervesces strongly to violently from the surface downward. Calcium carbonate equivalent probably in the range 20–40 percent.

C Canisteo—this is essentially calcareous Webster. As mapped, it may be noncalcareous in the surface, but carbonates must be detected somewhere in the 0–15 inch layer. It has lower calcium carbonate equivalent, heavier textures, and stronger development than Harps.

H⁻ Harps-Canisteo—an intergrade that has either Harps-like characteristics in the surface and becomes more Canisteo-like with depth or Canisteo-like surface characteristics and a Harps-like subsoil.

Wa Webster-Canisteo—an intergrade in which carbonates are first detected in the 15–22 inch layer. All other characteristics of Wa, W, and C are essentially the same.

C⁻ Inverted Canisteo-Heavy Webster—this represents a rather peculiar condition that tends to occur as a narrow band around the potholes. The surface is moderately to strongly calcareous, but carbonates decrease with depth to a noncalcareous, heavy, well-developed subsoil like that of heavy Webster.

G Glenco—a poorly drained soil that occupies small potholes, the outer portions of large potholes, or connecting drainage-ways. It has a black, highly organic surface but a gray, mineral, heavy, well-developed subsoil. In many respects it is similar to heavy Webster except for the organic surface and lack of grit and pebbles. Depth to carbonate is generally greater than 42 inches, but may be up to 36 inches.

Ga Calcareous Glenco—Glenco that becomes calcareous above 36 inches. It usually lacks the heavy textures and good development of regular Glenco as well.

O Okoboji—a black, mucky silt loam, very weakly developed soil occurring in the deepest areas of the potholes.

GO Glenco-Okoboji—an intergrade that may have the heavy textures of Glenco, but is darker, more organic, less well developed, and wetter than Glenco.

Seventeen soil series were recognized and mapped in the field, utilizing soil samples obtained with a 42-inch hand probe.

Data Analysis

General descriptive data. Data collected from quadrat studies, mapping studies, soil studies, and topographic studies were used to describe generally the vegetation. Frequency values and average cover values were determined for all species in every stand.

Ordination analysis. An ordination technique proposed by Orloci (1966) was employed to ordinate vegetation units within the different subcommunities listed above. Through this technique the entities to be ordinated (i.e., plant species or stands of vegetation) are projected as points into n-dimensional space. Such points are positioned by attribute scores through the application of the R and Q techniques of factor analysis. Once established, this multidimensional array of points is then reduced to a three dimensional system. This is accomplished by selecting the two most different stands or species and placing one at zero and the other at some distance along the abscissa. All other stands or species under consideration are then positioned linearly in relationship to these two extremes. This action thus establishes the X-axis. The above process is repeated until all points have been established in three dimensional space (i.e., Y and Z axes have been added). Coordinate values for the X, Y, and Z axes are given as output from the computer.

Interspecific association analysis. Expressions of interspecific association were attempted utilizing Cole's Index (1949). Step one in the computation of the index involves the accumulation of 2 × 2 contingency tables. Actual calculation of the index involves the following three sets of formulas:

when ad ≧ bc:

$$C_7 \pm {}_c = \frac{ad - bc}{(a + b)(b + d)} \quad \frac{(a + c)(c + d)}{n(a + b)(b + c)}$$

when bc > ad and d ≧ a:

$$C_7 \pm {}_c = \frac{ad - bc}{(a + b)(a + c)} \quad \frac{(b + d)(c + d)}{n(a + b)(a + c)}$$

when bc > ad and a > d:

$$C_7 \pm {}_c = \frac{ad - bc}{(b + d)(c + d)} \quad \frac{(a + b)(a + c)}{n(b + d)(c + d)}$$

where C_7 = Cole's Index of Interspecific Association

c = standard deviation Cole's Index

n = total number of samples

and a, b, c, and d represent the four cells of the 2 × 2 contingency table.

Tests of statistical significance were performed by means of the Chi-square test. The chi-squares were computed by the formula:

$$X^2 = \frac{(ad - bc)^2 n}{(a + b)(a + c)(c + d)(b + d)}$$

where X^2 = Chi-square value

n = number of samples

and a, b, c, and d represent the different cells of the 2 × 2 contingency table.

In all cases a single degree of freedom was used. Chi-square values greater than 3.84 were considered to be significant at the 5 percent level, and values greater than 6.63 were considered to be significant at the 1 percent level.

Data representation. Graphic representation of data obtained from topographic studies and from ordination analysis was drawn by the computer. Such representation was accomplished through the use of a plotting technique developed and programmed by Mr. Howard Jesperson, Agricultural Experimental Station, Iowa State University.

Results and Discussion

Species composition

Information on species sampled in the upland regions of Kalsow Prairie is presented in Table 1. Cover, composition (i.e., based on cover), and frequency values of *Sporobolus heterolepis, Andropogon gerardi, Poa pratensis,* and *Panicum leibergii* indicate these are the dominant grasses of the upland sites. Important or subdominant forbs include *Solidago canadensis, Solidago rigida, Helianthus grosseserratus, Amorpha canescens, Aster ericoides, Desmodium canadense, Zizia aurea, Helianthus laetiflorus, Aster laevis, Ratibida pinnata, Ceanothus americanus,* and *Rosa suffulta.*

Average cover values (Table 1) ranged from a high of 25.4 for *Sporobolus heterolepis* to a low of 0.01 for several species. Percentage frequency values, on the other hand, ranged from 73.1 for *Andropogon gerardi* to 0.1 for many species. No tests of correlation were made between average cover values and percentage frequency, but those species showing the highest cover values generally showed correspondingly higher percentage frequency values.

Since *Sporobolus heterolepis* is the dominant plant of the upland sites, Kalsow Prairie is placed within the "Consociation" designated by Weaver and Fitzpatrick (1934) as the Prairie Dropseed type (*Sporobolus heterolepis*). Weaver and Fitzpatrick (1934) described this particular consociation as being the least extensive and least important tall-grass subcommunity. It was found to occupy drier upland sites and included the two subcominants *Stipa spartea* and *Schizachyrium scoparius.* Although these two species were present (Table 1), they were not found in sufficient quantity to be labeled subdominants. The important grass species found with *Sporobolus heterolepis* in this study (i.e., *Andropogon gerardi, Poa pratensis,* and *Panicum leibergii*) suggest that the present-day upland regions of Kalsow Prairie are vegetatively distinct from the Prairie Dropseed Consociation of similar areas described earlier by Weaver. Both the species and their characteristics suggest that this difference is due either to change in the original vegetation, to differences in community characteristics, or to variations in the more recently glaciated land. *Poa pratensis,* for example, is an introduced species whose characteristics are such that it is able to compete well within the environment of prairie protected from fire and, under conditions of grazing, mowing, and other disturbance, is known to increase in importance (Weaver 1954). *Andropogon gerardi,* on the other hand, is a native grass described by Weaver and Fitzpatrick (1934) as the dominant of the most extensive tall-grass consociation that occupied the lowlands and lower moist slopes of the tall-grass prairie region.

Historical information, as well as evidence obtained in this study, indicates that much of the Kalsow Prairie has been subjected to

Table 1. Cover, composition, and frequency percentages for species sampled on upland prairie sites.

Species	Cover (%)	Composition (%)	Frequency (%)	Frequency[a] (%)
Sporobolus heterolepis	25.42	27.81	66.7	85.0
Andropogon gerardi	15.93	17.43	73.1	87.5
Poa pratensis	12.36	13.52	54.5	90.0
Solidago canadensis	4.12	4.51	38.9	15.0
Solidago rigida	2.57	2.81	19.4	5.0
Panicum leibergii	2.56	2.80	34.0	12.5
Helianthus grosseserratus	2.30	2.52	31.6	10.0
Amorpha canescens	2.08	2.28	15.0	27.5
Aster ericoides	1.99	2.19	40.7	37.5
Desmodium canadense	1.66	1.82	23.0	5.0
Zizia aurea	1.62	1.77	36.1	67.5
Helianthus laetiflorus	1.49	1.63	11.4	7.5
Aster laevis	1.30	1.42	16.9	7.5
Ratibida pinnata	1.26	1.39	20.6	10.0
Ceanothus americanus	1.15	1.26	.9	2.5
Rosa suffulta	1.07	1.17	18.4	45.0
Lysimachia hybrida	.84	.92	.7	5.0
Convolvulus sepium	.76	.83	1.2	2.5
Silphium laciniatum	.72	.79	12.4	15.0
Achillea lanulosa	.68	.74	11.7	45.0
Galium obtusum	.65	.71	29.1	5.0
Spartina pectinata	.60	.66	10.3	17.5
Artemisia ludoviciana	.59	.65	4.4	2.5
Comandra umbellata	.59	.65	9.1	45.0
Schizachyrium scoparius	.52	.57	1.7	85.0
Fragaria virginiana	.52	.57	20.7	7.5
Physalis heterophylla	.47	.51	2.1	
Elymus canadensis	.45	.49	19.4	12.5
Stipa spartea	.45	.49	6.6	20.0
Aster simplex	.43	.47	13.1	
Muhlenbergia racemosa	.37	.40	11.2	
Panicum virgatum	.36	.39	12.1	75.0
Senecio pauperculus	.36	.39	9.3	
Lithospermum canescens	.35	.38	13.0	17.5
Heliopsis helianthoides	.31	.34	5.8	17.5
Psoralea argophylla	.29	.32	3.8	5.0
Solidago missouriensis	.28	.31	2.7	5.0
Apocynum sibiric...	.27	.30	3.3	
Asclepias tuberosa	.26	.28	3.5	2.5
Setaria viridis	.23	.25	.7	
Cirsium altissimum	.23	.25	4.6	17.5
Sorghastrum nutans	.21	.23	5.4	42.5
Liatris pycnostachya	.21	.23	9.8	27.5
Petalostemum purpureum	.20	.22	29.5	32.5
Pycnanthemum virginianum	.20	.22	7.0	5.0
Lythrum alatum	.20	.22	.6	
Phlox pilosa	.16	.18	6.3	10.0
Physalis virginiana	.16	.18	3.1	7.5
Viola pedatifida	.14	.15	5.5	5.0
Setaria lutescens	.13	.14	.5	
Viscia americana	.12	.13	4.7	7.5
Lathyrus venosus	.12	.13	2.5	5.0
Equisetum kansanum	.11	.12	4.7	42.5
Eryngium yuccifolium	.11	.12	1.0	2.5
Petalostemum candidum	.11	.12	3.9	7.5

[a]Figures taken from Moyer (1953) for comparison purposes.

Table 1 continued.

Species	Cover (%)	Composition (%)	Frequency (%)	Frequency[a] (%)
Baptisia leucophaea	.09	.10	.7	15.0
Asclepias syriaca	.07	.08	1.4	
Ambrosia artemisifolia	.06	.07	1.4	
Baptisia leucantha	.06	.07	.7	
Carex gravida	.06	.07	2.0	
Oxalis stricta	.06	.07	.9	
Teucrium canadense	.06	.07	1.7	
Viola sp.	.06	.07	3.2	
Gentiana andrewsii	.05	.06	1.1	2.5
Potentilla arguta	.05	.06	.5	
Scutellaria leonardii	.05	.06	2.2	
Thalictrum dasycarpum	.05	.06	1.6	7.5
Lespedeza capitata	.04	.04	1.0	2.5
Solidago riddellii	.04	.04	2.4	
Anemone cylindrica	.03	.03	.5	35.0
Helenium autumnale	.03	.03	.8	
Pedicularis canadensis	.03	.03	1.2	22.5
Bouteloua curtipendula	.03	.03	.9	7.5
Chenopodium album	.02	.02	.2	
Lathyrus palustris	.02	.02	1.1	
Liatris aspera	.02	.02	.8	25.0
Lycopus americanus	.02	.02	.7	
Lysimachia chiliata	.02	.02	.6	
Mentha arvensis	.02	.02	.4	
Solidago gymnospermoides	.02	.02	1.4	5.0
Vernonia fasciculata	.02	.02	.3	
Taraxacum officinale	.02	.02	.9	
Echinacea pallida	.02	.02	.4	10.0
Agropyron repens	.01	.01	.5	
Agropyron smithii	.01	.01	1.2	2.5
Anemone canadensis	.01	.01	1.7	
Arabis hirsuta	.01	.01	.1	
Asclepias sullivantii	.01	.01	.2	5.0
Asclepias verticillata	.01	.01	.4	2.5
Astragalus canadensis	.01	.01	.3	
Cicuta maculata	.01	.01	.3	10.0
Helianthus maximiliani	.01	.01	.6	
Juncus tenuis	.01	.01	.1	
Lactuca scariola	.01	.01	.4	
Lysimachia quadriflora	.01	.01	.8	
Panicum capillare	.01	.01	.1	
Phleum pratense	.01	.01	.6	85.0
Rudbeckia hirta	.01	.01	.3	
Veronicastrum virginicum	.01	.01	.1	
Allium sp.	.01	.01	.1	
Aster novae-angliae	.01	.01	.4	
Cacalia tuberosa	.01	.01	.1	
Prenanthes racemosa	.01	.01	.7	
Solidago nemoralis	.01	.01	2.6	2.5
Trifolium pratense	.01	.01	.1	12.5

[a]Figures taken from Moyer (1953) for comparison purposes.

mowing, grazing to some extent, and abundant pocket gopher activity. Both Mima mounds and pocket gopher (*Geomys bursanins*) activity are widely scattered across the prairie. The Mima mounds are poorly understood areas of disturbance. Other disturbance areas are along the south and west boundaries of the prairie, where dust from adjacent plowed fields has been deposited in depths up to two or three feet.

The distribution of soil types in the 8 ha intensive study site is here of interest. Our survey showed that much of the 8 ha is of lowland soil types. In fact, a large part of the upland prairie may occupy lowland soil types. The disturbance will give possible explanation to the high incidence of *Poa pratensis* found with *Sporobolus heterolepis*, and the large tracts of lowland soil types might well explain the abundance of *Andropogon* *gerardi.* Why *Sporobolus heterolepis* is found growing in such abundance on the lowland areas is difficult to explain, but it might be due to the high amount of calcareous soil types found within Kalsow Prairie.

Early studies (Weaver and Fitzpatrick 1934, Shimek 1925) suggest the distribution of *Sporobolus heterolepis* as restricted to driest uplands. Because these areas often show a lack of soil profile development or outcroppings of parent material often high in carbonates (Oschwald et al., 1965), it is feasible that *Sporobolus heterolepis* is adapted to grow on soils of high carbonate content and that it might easily be extended to lowland soils high in carbonate content.

Moyer (1953), in a study of the Kalsow Prairie vegetation, gave percentage frequency values for many of the species included in Table 1 of this paper. His figures are reported in column four of Table 1 for comparison. These figures suggest that there have been some changes in the species composition of the upland prairie since 1953. Some of the species that show increases in percentage frequency in the past are *Solidago canadensis, Solidago rigida, Panicum leibergii, Helianthus grosseserratus, Desmodium canadense, Galium obtusum,* and *Fragaria virginiana.* Species that show decreases in percentage frequency over this same period are *Phleum pratense, Poa pratensis, Zizia aurea, Rosa suffulta, Schizachyrium scoparius, Panicum virgatum, Sorghastrum nutans, Equisetum kansanum, Anemone cylindrica, Liatris aspera,* and *Sporobolus heterolepis.* Such changes are not easily explained but might be related to general fluctuations of the vegetation over a period of years, to fluctuations in climatic conditions (i.e., time and duration of rainfall, drought, etc.), to interspecific competition, to differences in the technique and intensity of sampling, and to the possible influence of slight disturbance upon the prairie due to increased populations of pocket gophers, dust accumulation from adjacent fields, public visitors, and management practices.

To describe in greater detail the interrelationships of species in the upland prairie a three-dimensional stand and species ordination treatment was attempted using Orloci's (1966) method. The results are shown in Figures 2, 3, and 4. Data used in the ordination

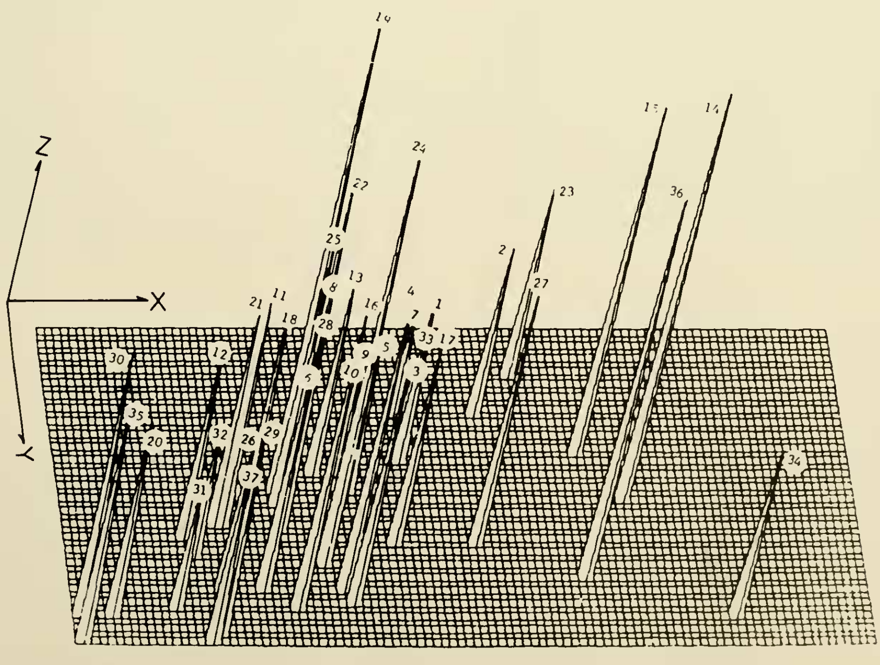

Fig. 2. Three-dimensional ordination of 37 upland prairie sites.

were from 444 samples taken from 37 sites in the upland prairie community. These 37 sites are shown as points in three-dimensional space in Figure 2 and as dots in two-dimensional space in Figure 3. Initially, attempts were made to place the individual sites into specific groups. Groups were designated on the basis of where the stands fell when plotted in three-dimensional space (i.e., those sites which fell close together were considered to be the most similar and were placed within the same group). Attempts to understand the meaning of such groupings were unsuccessful. Further attempts to understand the ordering pattern led to the conclusion that discrete grouping within these upland prairie regions is not feasible. It appears that the ordering of the stands into three-dimensional space was controlled by the response of several of the major species to environmental gradients. Of these species, *Andropogon gerardi* (Fig. 5) and *Sporobolus heterolepis* (Fig. 6) were plotted against the X and Y coordinates of the ordination. As can be seen, both species show continuous distribution in relationship to the axes. Stands plotted near the origin and adjacent to the Y-axis were found to be from drier sites, and those found away from the origin were found on wetter, more moist sites. These facts tend to support the hypothesis that the vegetation of the upland prairie is a continuum as earlier described by Curtis (1955) and Dix and Butler (1960). Kennedy (1969), in studying an upland prairie in Guthrie County, Iowa, also concluded that prairie vegetation there is best described through the use of the continuum-index concept.

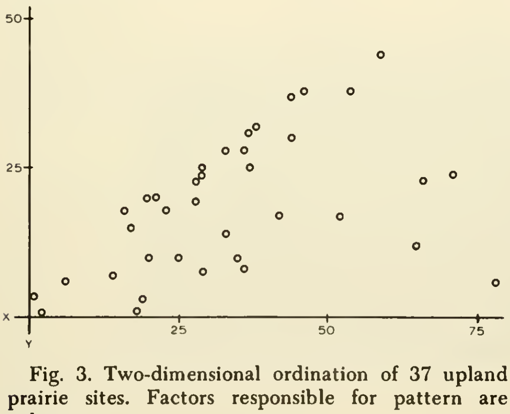

Fig. 3. Two-dimensional ordination of 37 upland prairie sites. Factors responsible for pattern are unknown.

Attempts at environmental factor correlation with the ordination axes were not made since only general information on environmental gradients was available. It seems, however, that these axes represent environmental gradients and that the ordering of stands or species along these axes is accomplished through the response of the different stands or species to certain factors such as moisture, texture, soil carbonates, or other soil factors.

The species ordination is shown in Figure 4. *Spartina pectinata* and *Ceanothus americanus* are the most different entities on the X-axis, and *Andropogon gerardi* is the most distinct entity on the Y-axis. Other species having distinct distribution patterns are *Physalis virginiana, Silphium laciniatum, Oxalis stricta, Amorpha canescens, Solidago missouriensis, Desmodium canadense, Helianthus grosseserratus, Aster ericoides, Vicia americana, Pycnanthemum virginianum, Ratibida pinnata, Aster laevis,* and *Helianthus laetiflorus.* All other species either showed no definite distribution patterns or were too rare to establish a meaningful pattern. The circles A, B, and C in Figure 4 represent the points where 76 of the 92 species fell. This ordering of species has not delineated associated groups but has pointed out

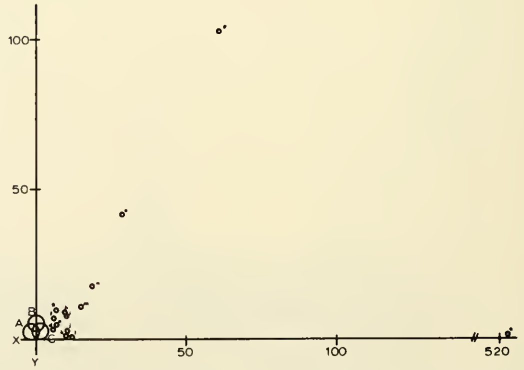

Fig. 4. Two-dimensional ordination of species found in upland prairie study sites, factors responsible for patterns unknown: A, B, and C. = Clusters of species not showing distinct distribution patterns. d. = *Helianthus laetiflorus*. e. = *Aster laevis*. f. = *Ratibida pinnata*. g. = *Pycnanthemum virginianum*. h. = *Aster ericoides*. i. = *Vicia americana*. j. = *Helianthus grosseserratus*. k. = *Desmodium canadense*. l. = *Amorpha canescens*. m. = *Oxalis stricta*. n. = *Silphium laciniatum*. o. = *Physalis virginiana*. p. = *Andropogon gerardi*. q. = *Spartina pectinata*.

those species that exhibit peculiar distribution patterns or that show a definite response to one or several environmental stimuli. Sanders (1969) found that the R-analysis of Orloci (1966) did give him some fairly distinct groups of associated species as well as groups of species that could not be considered associated. Collins (1968) used the technique to identify taxa that were distinct and different and used them as indicator species in his interpretation of the ecological relationships of fossil diatom populations. It is evident from Figure 4 that the method has not provided information on groups of associated species but rather has indicated taxa that are distinct and therefore may have some usefulness as indicator species.

Attempts to discover groups of positively associated species within the upland regions of Kalsow Prairie were made using Cole's Index (1949). Those species showing positive association with other taxa are shown in Table 2. A total of 298 significant associations were found. Some species, such as *Achillea lanulosa, Agropyron smithii, Amorpha canescens, Andropogon gerardi, Asclepias tuberosa, Carex gravida, Comandra umbellata, Helenium autumnale, Lespedeza capitata, Phleum pratense,* and *Solidago gymnospermoides,* exhibit positive association with only a limited number of species. Other species, however, show positive association with a large number of species. Some of these species are *Aster ericoides, Desmodium canadense, Fragaria virginiana, Galium obtusum, Helianthus grosseserratus, Poa pratensis, Solidago canadensis, Solid-go rigida, Sporobolus heterolepis,* and *Zizia aurea.* Many species showed no significant association or expressed values of high negative association. Positive values of Cole's Index indicate that species occur together more often than would otherwise be expected due to chance (Hale 1955, Hurlbert 1969). Therefore, through the use of such an index one can deduce groups of species that consistently show positive values of association with one another. Figures 7, 8, and 9 were constructed from values taken from Table 2 to illustrate the existence of such groups within the upland prairie. In all three cases one species was picked and the corresponding figure was then built up around this species.

Species Distribution Patterns

Eight hectares of the prairie adjacent to its southern boundary (Figure 1) were selected for intensive study of the distribution of plant species in relation to soils and topography. The area was chosen because it included within its boundaries a representation of all vegetation types occurring on Kalsow Prairie. The area was staked on a 9 × 9 m grid that placed 968 points within the 8 ha. From these points all factors included in this study were examined.

The presence of all plant species found in the area was recorded in relation to each 27 square-meter section of the grid. From these present figures, distribution maps for 160 species were constructed. Examples of these maps are shown in Figures 10A through 10HH. These figures illustrate examples of distribution patterns often shared by several species. *Andropogon gerardi* (Fig. 10D) illustrates a type of pattern typical of many species commonly found in the upland prairie.

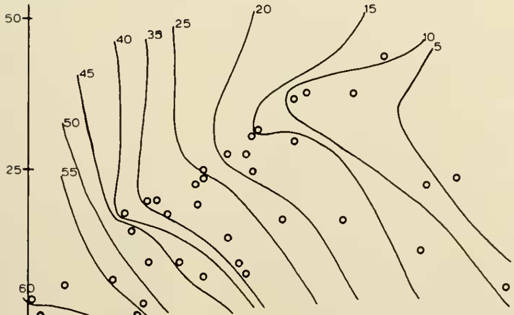

Fig. 5. Two-dimensional ordination of upland prairie with percentage cover values of *Sporobolus heterolepis* for each site shown relating directly to the Y-axis.

Fig. 6. Two-dimensional ordination of upland prairie with percentage cover values of *Andropogon gerardi* for each site shown relating directly to the X-axis.

Table 2. Cole's Index values expressing positive interspecific association on upland prairie.

Species	Species	X^{2a}	$C_7{}^b$	$\sigma_7{}^c$
Achillea lanulosa	*Andropogon gerardi*	18.77	.73	.17
	Aster ericoides	6.84	.22	.08
	Poa pratensis	5.03	.27	.11
	Solidago rigida	13.41	.21	.05
	Sporobolus heterolepis	11.06	.51	.15
Agropyron repens	*Carex gravida*	4.91	.22	.09
	Convolvulus sepium	7.04	.44	.16
	Physalis heterophylla	5.31	.22	.09
Agropyron smithii	*Andropogon gerardi*	5.96	.73	.29
	Aster ericoides	8.97	.45	.15
	Galium obtusum	4.33	.34	.16
	Helianthus grosseserratus	5.43	.43	.18
	Muhlenbergia racemosa	24.25	.27	.05
	Petalostemum purpureum	8.26	.20	.06
	Pycnanthemum virginianum	5.65	.18	.07
	Solidago canadensis	13.22	.53	.14
	Solidago riddellii	25.22	.24	.04
Ambrosia artemisifolia	*Asclepias syriaca*	83.22	.43	.04
	Helianthus grosseserratus	5.12	.23	.10
	Senecio pauperculus	155.77	.77	.06
	Setaria lutescens	58.48	.28	.03
	Setaria viridis	165.69	.57	.04
	Stipa spartea	4.00	.24	.12
	Taraxacum officinale	172.49	.55	.04
Amorpha canescens	*Andropogon gerardi*	15.62	.51	.13
	Panicum leibergii	28.29	.24	.04
	Solidago rigida	19.00	.20	.04
	Sporobolus heterolepis	41.54	.77	.11
Andropogon gerardi	*Aster ericoides*	126.73	.18	.01
	Poa pratensis	176.68	.30	.02
	Solidago canadensis	85.47	.15	.01
	Sporobolus heterolepis	238.41	.46	.02
Schizachyrium scoparius	*Comandra umbellata*	10.40	.21	.06
	Lithospermum canescens	19.30	.35	.08
	Panicum leibergii	5.62	.41	.17
	Petalostemum purpureum	7.53	.18	.06
	Phlox pilosa	11.12	.19	.05
	Solidago rigida	6.01	.25	.10
	Sporobolus heterolepis	8.23	.77	.26
	Zizia aurea	5.23	.31	.13
Anemone canadensis	*Artemisia ludoviciana*	5.53	.19	.08
	Petalostemum candidum	6.16	.19	.07
	Poa pratensis	5.57	.80	.33
	Solidago missouriensis	25.23	.16	.03
Apocynum sibiricum	*Aster simplex*	14.68	.26	.06
	Calamagrostis canadensis	102.95	.70	.06
	Carex aquatilis	44.71	.35	.05
	Carex retrorsa	70.51	.55	.06
	Carex lasiocarpa	66.57	.39	.04
	Fragaria virginiana	3.83	.38	.19
	Heliopsis helianthoides	4.39	.27	.12
	Polygonum coccimeum	15.26	.18	.04
	Spartina pectinata	13.73	.18	.05
Artemisia ludoviciana	*Aster ericoides*	4.53	.42	.19
	Convolvulus sepium	51.32	.22	.03
	Helianthus laetiflorus	14.98	.28	.07
	Poa pratensis	15.37	.78	.19
Asclepias sullivantii	*Elymus canadensis*	5.94	.67	.27

[a]Chi-square
[b]Cole's Index
[c]Standard deviation Cole's Index

Table 2 continued.

Species	Species	X^{2a}	$C_7{}^b$	$\sigma_7{}^c$
Asclepias syriaca	*Aster simplex*	4.71	.38	.17
	Cirsium altissimum	5.77	.21	.08
	Desmodium canadense	9.84	.66	.21
	Equisetum kansanum	6.87	.21	.08
	Lithospermum canescens	8.15	.31	.10
	Rosa suffulta	9.99	.32	.10
	Senecio pauperculus	47.45	.43	.06
	Taraxacum officinale	25.23	.20	.04
	Thalictrum dasycarpum	12.88	.23	.06
Asclepias tuberosa	*Aster ericoides*	4.80	.27	.12
	Desmodium canadense	17.17	.42	.10
	Elymus canadensis	9.21	.29	.09
	Sporobolus heterolepis	17.15	.92	.22
	Zizia aurea	7.13	.30	.11
Asclepias verticillata	*Lithospermum canescens*	14.39	1.00	.26
Aster ericoides	*Helianthus grosseserratus*	17.76	.17	.03
	Poa pratensis	105.26	.46	.04
	Solidago canadensis	49.17	.22	.03
	Sporobolus heterolepis	70.97	.49	.05
	Zizia aurea	40.95	.19	.02
Aster laevis	*Desmodium canadense*	23.69	.30	.06
	Panicum leibergii	53.78	.36	.04
	Poa pratensis	27.26	.54	.10
	Sporobolus heterolepis	9.76	.41	.13
Aster simplex	*Calamagrostis canadensis*	42.41	.21	.03
	Carex gravida	34.75	.21	.03
	Carex retrorsa	30.80	.17	.03
	Fragaria virginiana	4.89	.19	.08
	Galium obtusum	54.31	.37	.05
	Helianthus grosseserratus	95.05	.56	.05
	Poa pratensis	7.48	.58	.21
	Senecio pauperculus	61.08	.19	.02
	Silphium laciniatum	32.99	.29	.05
	Spartina pectinata	34.20	.32	.05
Bouteloua curtipendula	*Comandra umbellata*	5.23	.29	.12
	Helianthus laetiflorus	7.18	.41	.15
	Phlox pilosa	7.47	.31	.11
Calamagrostis canadensis	*Carex aquatilis*	427.86	.50	.02
	Carex retrorsa	580.80	.74	.03
	Carex lasiocarpa	404.31	.45	.02
	Phalaris arundinacea	171.76	.20	.01
	Polygonum coccineum	64.45	.18	.02
	Spartina pectinata	154.17	.30	.02
Carex atherodes	*Carex retrorsa*	18.21	.27	.06
	Polygonum coccineum	370.61	.87	.04
	Scirpus fluviatilis	145.67	.34	.02
Carex aquatilis	*Carex retrorsa*	469.33	.88	.04
	Carex lasiocarpa	406.70	.59	.02
	Phalaris arundinacea	57.45	.16	.01
	Polygonum coccineum	33.93	.17	.02
	Spartina pectinata	66.04	.26	.03
Carex gravida	*Desmodium canadense*	17.26	.49	.11
	Fragaria virginiana	30.76	.64	.11
	Galium obtusum	21.59	.56	.11
	Helianthus grosseserratus	36.90	.71	.11
	Liatris pycnostrachya	8.21	.22	.07
	Muhlenbergia racemosa	4.90	.23	.10
	Petalostemum purpureum	9.82	.23	.07

[a]Chi-square
[b]Cole's Index
[c]Standard deviation Cole's Index

Table 2 continued.

Species	Species	X^{2a}	$C_7{}^b$	$\sigma_7{}^c$
	Silphium laciniatum	19.94	.30	.06
	Solidago canadensis	6.94	.57	.21
Carex lasiocarpa	*Lathyrus palustris*	110.24	1.00	.09
	Lysimachia hybrida	147.33	1.00	.08
	Phalaris arundinacea	92.24	.21	.02
	Polygonum coccineum	27.12	.17	.03
	Spartina pectinata	72.67	.30	.03
Carex retrorsa	*Carex lasiocarpa*	465.71	.50	.02
	Phalaris arundinacea	158.23	.20	.01
	Polygonum coccineum	79.04	.20	.02
	Spartina pectinata	117.52	.27	.02
Cirsium altissimum	*Fragaria virginiana*	8.78	.21	.07
	Galium obtusum	7.65	.29	.10
	Helianthus grosseserratus	8.53	.34	.11
	Petalostemum candidum	8.80	.15	.05
	Physalis virginiana	24.36	.28	.05
	Solidago canadensis	5.09	.21	.09
Comandra umbellata	*Desmodium canadense*	47.92	.50	.07
	Elymus canadensis	11.91	.23	.06
	Fragaria virginiana	15.97	.26	.06
	Panicum leibergii	16.18	.24	.05
	Petalostemum purpureum	19.78	.18	.03
	Poa pratensis	10.28	.39	.12
	Ratibida columnifera	26.47	.26	.05
	Solidago rigida	15.47	.23	.05
	Sporobolus heterolepis	15.25	.62	.15
	Zizia aurea	28.32	.43	.08
	Solidago nemoralis	32.92	.17	.02
Convolvulus sepium	*Poa pratensis*	5.30	.66	.28
Desmodium canadense	*Elymus canadensis*	80.81	.27	.02
	Fragaria virginiana	75.91	.40	.04
	Galium obtusum	81.55	.43	.04
	Helianthus grosseserratus	26.91	.24	.04
	Muhlenbergia racemosa	31.07	.23	.04
	Poa pratensis	38.84	.34	.05
	Solidago rigida	20.28	.21	.04
	Sporobolus heterolepis	99.46	.70	.06
	Zizia aurea	66.09	.29	.03
Elymus canadensis	*Fragaria virginiana*	72.47	.27	.03
	Galium obtusum	21.27	.26	.05
	Poa pratensis	44.15	.39	.05
	Sporobolus heterolepis	42.70	.49	.07
Equisetum kansanum	*Heliopsis helianthoides*	7.25	.19	.07
	Lithospermum canescens	20.66	.20	.04
	Petalostemum candidum	11.42	.21	.06
	Phlox pilosa	6.58	.19	.07
	Sporobolus heterolepis	20.81	.83	.18
	Zizia aurea	11.12	.31	.09
Eryngium yuccifolium	*Panicum leibergii*	7.80	.31	.11
	Rosa suffulta	10.29	.22	.06
	Solidago rigida	4.57	.24	.11
	Sporobolus heterolepis	7.90	.85	.30
Fragaria virginiana	*Galium obtusum*	69.59	.39	.04
	Helianthus grosseserratus	40.39	.31	.04
	Muhlenbergia racemosa	37.67	.26	.04
	Poa pratensis	29.55	.33	.05
	Solidago canadensis	13.28	.33	.08
	Sporobolus heterolepis	39.10	.48	.07
	Zizia aurea	4.89	.18	.08

[a]Chi-square
[b]Cole's Index
[c]Standard deviation Cole's Index

Table 2 continued.

Species	Species	X^{2a}	C_7[b]	σ_7[c]
Galium obtusum	*Helianthus grosseserratus*	91.71	.35	.03
	Muhlenbergia racemosa	25.27	.21	.04
	Silphium laciniatum	41.48	.17	.02
	Solidago canadensis	13.09	.31	.08
	Zizia aurea	5.17	.18	.07
Gentiana andrewsii	*Heliopsis helianthoides*	12.46	.45	.12
	Liatris pycnostachya	4.04	.26	.13
	Lithospermum canescens	4.52	.40	.18
	Zizia aurea	4.34	.71	.34
Helenium autumnale	*Helianthus grosseserratus*	15.18	.88	.22
	Lythrum alatum	48.25	.19	.02
	Muhlenbergia racemosa	10.43	.22	.06
	Poa pratensis	11.28	.86	.25
	Pycnanthemum virginianum	7.30	.25	.09
	Senecio pauperculus	40.42	.62	.09
	Solidago canadensis	5.32	.41	.17
Helianthus grosseserratus	*Solidago canadensis*	73.49	.21	.02
Helianthus laetiflorus	*Panicum leibergii*	42.24	.37	.05
	Phlox pilosa	25.63	.18	.03
	Sporobolus heterolepis	5.53	.36	.15
Helianthus maximiliana	*Scutellaria leonardii*	11.06	.19	.05
	Taraxacum officinale	11.06	.19	.05
Heliopsis helianthoides	*Poa pratensis*	6.77	.52	.19
	Pycnanthemum virginianum	20.89	.32	.07
	Ratibida pinnata	6.37	.21	.08
	Solidago canadensis	8.97	.41	.13
Lactuca scariola	*Pedicularis canadensis*	12.13	.19	.05
	Rosa suffulta	7.31	.35	.12
Lathyrus palustris	*Lysimachia hybrida*	35.58	.24	.04
	Senecio pauperculus	3.94	.21	.10
	Silphium laciniatum	10.63	.46	.14
	Spartina pectinata	14.78	.39	.10
	Viola sp.	6.30	.23	.08
Lespedeza capitata	*Lithospermum canescens*	12.60	.45	.12
	Panicum leibergii	3.80	.38	.19
	Rosa suffulta	5.52	.28	.11
	Silphium laciniatum	5.93	.28	.11
Liatris aspera	*Physalis virginiana*	21.69	.40	.08
Liatris pycnostachya	*Poa pratensis*	6.21	.24	.09
	Silphium laciniatum	17.79	.19	.04
	Solidago canadensis	17.40	.28	.06
	Sporobolus heterolepis	39.56	.78	.12
	Zizia aurea	26.25	.32	.06
Lithospermum canescens	*Panicum leibergii*	26.20	.25	.04
	Sporobolus heterolepis	37.09	.81	.13
	Zizia aurea	23.59	.33	.06
Lycopus americanus	*Lythrum alatum*	52.06	.21	.02
	Senecio pauperculus	18.03	.43	.10
	Spartina pectinata	19.71	.43	.09
Lysimachia hybrida	*Muhlenbergia racemosa*	5.77	.60	.25
	Polygonum coccineum	53.59	1.00	.13
	Scirpus fluviatilis	95.59	.83	.08
	Spartina pectinata	13.03	.64	.17
	Viola sp.	9.00	.31	.10
Lysimachia quadriflora	*Muhlenbergia racemosa*	8.08	.22	.07
	Pedicularis canadensis	54.24	.50	.06
	Petalostemum purpureum	4.08	.20	.09
	Poa pratensis	4.41	.63	.30
	Senecio pauperculus	17.76	.48	.11

[a]Chi-square
[b]Cole's Index
[c]Standard deviation Cole's Index

Table 2 continued.

Species	Species	X^{2a}	C_7^b	σ_7^c
Lythrum alatum	*Senecio pauperculus*	5.70	.27	.11
	Spartina pectinata	6.37	.28	.11
Mentha arvensis	*Phalaris arundinacea*	6.67	.21	.08
	Polygonum coccineum	6.64	.30	.11
Muhlenbergia racemosa	*Zizia aurea*	7.48	.25	.09
Panicum capillare	*Pycnanthemum virginianum*	20.53	.20	.04
	Senecio pauperculus	27.20	.24	.04
	Silphium laciniatum	12.59	.20	.05
	Solidago canadensis	6.31	.21	.08
	Zizia aurea	11.91	.28	.08
Panicum leibergii	*Poa pratensis*	12.96	.24	.06
	Sporobolus heterolepis	56.41	.65	.08
Panicum virgatum	*Poa pratensis*	12.96	.24	.06
	Sporobolus heterolepis	56.41	.65	.08
Pedicularis canadensis	*Pycnanthemum virginianum*	37.72	.49	.07
	Senecio pauperculus	5.78	.22	.09
	Solidago rigida	5.11	.29	.12
	Zizia aurea	20.45	.79	.17
Petalostemum candidum	*Ratibida pinnata*	4.02	.21	.10
	Rosa suffulta	4.27	.23	.10
Petalostemum purpureum	*Poa pratensis*	11.86	.34	.09
	Solidago canadensis	16.33	.28	.06
	Solidago rigida	20.61	.22	.04
	Sporobolus heterolepis	30.35	.71	.12
	Zizia aurea	24.91	.33	.06
Phalaris arundinacea	*Polygonum coccineum*	78.87	.41	.04
	Spartina pectinata	25.65	.26	.05
Phleum pratense	*Phlox pilosa*	5.50	.34	.14
	Ratibida pinnata	7.39	.73	.26
Phlox pilosa	*Ratibida pinnata*	8.27	.25	.08
	Sporobolus heterolepis	7.60	.64	.23
Physalis virginiana	*Rosa suffulta*	5.93	.21	.08
	Solidago rigida	4.93	.32	.14
Poa pratensis	*Sporobolus heterolepis*	54.66	.31	.04
Polygonum coccineum	*Scirpus fluviatilis*	350.08	.37	.01
Potentilla arguta	*Solidago missouriensis*	5.48	.30	.12
Psoralea argophylla	*Stipa spartea*	6.50	.18	.07
Pycnanthemum virginianum	*Senecio pauperculus*	30.62	.19	.03
	Silphium laciniatum	25.56	.21	.04
	Solidago canadensis	25.73	.31	.06
	Sporobolus heterolepis	11.25	.39	.11
	Zizia aurea	7.48	.69	.25
Ratibida pinnata	*Sporobolus heterolepis*	22.69	.48	.10
	Zizia aurea	19.66	.23	.05
Rosa suffulta	*Sporobolus heterolepis*	13.85	.54	.14
Rudbeckia hirta	*Solidago rigida*	7.17	.75	.28
Senecio pauperculus	*Solidago canadensis*	51.17	.42	.05
	Taraxacum officinale	100.89	.32	.03
Setaria lutescens	*Setaria viridis*	525.50	.89	.03
Silphium laciniatum	*Solidago canadensis*	4.85	.34	.15
	Spartina pectinata	15.95	.21	.05
	Sporobolus heterolepis	32.83	.52	.09
	Viola sp.	38.07	.19	.03
	Zizia aurea	43.57	.31	.04
Solidago canadensis	*Sporobolus heterolepis*	21.62	.28	.06
Solidago gymnospermoides	*Solidago rigida*	3.87	.22	.11
	Sporobolus heterolepis	8.50	.86	.29
	Zizia aurea	9.77	.47	.15

[a]Chi-square
[b]Cole's Index
[c]Standard deviation Cole's Index

Table 2 continued.

Species	Species	X^{2a}	C_7^b	σ_7^c
Solidago rigida	*Sporobolus heterolepis*	96.94	.84	.08
Sorghastrum nutans	*Sporobolus heterolepis*	17.68	.81	.19
	Zizia aurea	5.46	.23	.09
Sporobolus heterolepis	*Zizia aurea*	130.17	.19	.01
Viola sp.	*Zizia aurea*	8.97	.35	.11
Panicum implicatum	*Solidago nemoralis*	8.63	.19	.06

[a]Chi-square
[b]Cole's Index
[c]Standard deviation Cole's Index

This pattern indicates that these species have wide ecological amplitudes and are limited basically by conditions peculiar to the drainage areas of the prairie. Other species that showed similar distribution patterns were *Aster ericoides, Elymus canadensis, Equisetum kansanum, Lithospermum canescens, Petalostemum purpureum, Poa pratensis, Ratibida pinnata, Rosa suffulta, Solidago canadensis, Solidago rigida, Sporobolus heterolepis,* and *Zizia aurea.*

A pattern closely resembling that of *Andropogon gerardi* but also showing limited distribution on the higher and drier ridges of the area is that exemplified by *Silphium laciniatum* (Fig. 10J). Species included under this type of pattern were *Desmodium canadense, Fragaria virginiana, Galium obtusum, Helianthus grosseserratus, Heliopsis helianthoides, Liatris pycnostachya, Panicum virgatum,* and *Spartina pectinata.*

The pattern showed by *Ambrosia artemisifolia* (Fig. 10B) is limited to the border weed communities. Other species found limited to these areas were *Amaranthus tamariscinus, Ambrosia trifida, Brassica nigra, Chenopodium album, Helianthus annuus, Polygonum pennsylvanicum, Polygonum persicaria, Setaria lutescens,* and *Setaria viridis.*

Figure 10C (*Amorpha canescens*) illustrates a pattern common to species limited to growth on the ridges and lower slopes of the area. This would correspond to areas composed mainly of Clarion, Nicollet, and Webster soil types (Fig. 11). When compared with the pattern exhibited by *Andropogon gerardi,* this type shows a narrowing ecological amplitude and decrease in the ability of species exhibiting this type of pattern to compete in lowland areas. Other species showing this type of pattern were *Achillea lanulosa, Arabis hirsuta, Asclepias syriaca, Asclepias tuberosa, Aster laevis,* and *Panicum leibergii.*

Several species found limited in distribution to the mid- and upland slopes of the prairie exemplify the pattern shown by *Solidago nemoralis* (Fig. 10E). These species were *Eryngium yuccifolium, Solidago gymnospermoides, Solidago riddellii,* and *Viola pedatifida.* Such species show rather narrow ecological amplitudes when compared with the groups discussed earlier.

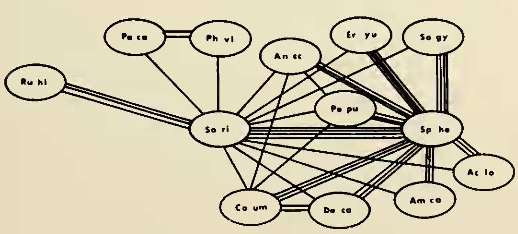

Fig. 7. *Solidago rigida* and associated species of upland prairie as determined by Cole's (1949) Index, the more lines between species, the greater the association. So ri = *Solidago rigida,* Ru hi = *Rudbeckia hirta,* Pe ca = *Pedicularis canadensis,* Ph vi = *Physalis virginiana,* An Sc = *Schizachyrium scoparius,* Er yu = *Eryngium yuccifolium,* Pe pu = *Petalostemum purpureum,* So gy = *Solidago gymnospermoides,* Sp he = *Sporobolus heterolepis,* Ac la = *Achillea lanulosa,* Am ca = *Amorpha canescens,* De ca = *Desmodium canadense,* Co um = *Comandra umbellata.*

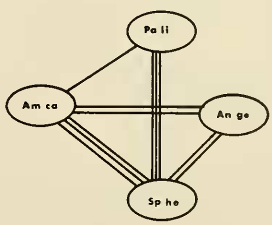

Fig. 8. *Amorpha canescens* and associated species of upland prairie as determined by Cole's (1949) Index, the more lines between the species, the greater the association. Am ca = *Amorpha canescens,* Pa li = *Panicum leibergii,* An ge = *Andropogon gerardi,* Sp he = *Sporobolus heterolepis.*

Another group exhibiting rather narrow ranges in distribution are characterized by the patterns shown in Figures 10N and 100. These species, *Artemisia ludoviciana, Ceanothus americanus, Echinacea pallida, Helianthus laetiflorus, Lathyrus venosus, Lespedeza capitata, Liatris aspera, Petalostemum candidum, Potentilla arguta, Psoralea argophylla, Solidago missouriensis*, and *Stipa spartea*, are found occupying the ridges and drier sites of the prairie. This would correspond to the Clarion, Clarion-Nicollet, and Nicollet areas of Figure 11.

A final group of species limited from growth in the drainage areas of the prairie show a pattern characteristic of those found in Figure 10A (*Agropyron smithii*) and Figure 10F (*Helenium autumnale*). Here again the ecological amplitudes of these species are narrow when compared with Andropogon *gerardi* or *Sporobolus heterolepis*. As can be seen, the distribution of these species corresponds closely to the borders of the pothole and drainage complex; thus these species mainly occupy soils that are characterized by being highly calcareous to the surface. Other species exhibiting this type of distribution are *Agrostis alba, Aster simplex, Lycopus americanus, Lysimachia quadriflora, Lythrum alatum, Senecio pauperculus* and *Viola* sp.

Species restricted in occurrence to the potholes and drainage ways of the area were found to exhibit two types of distributional patterns. The first, shown by *Calamagrostis*

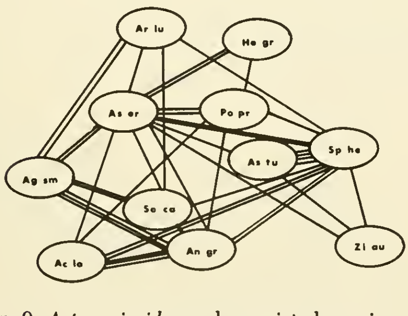

Fig. 9. *Aster ericoides* and associated species of upland prairie as determined by Cole's (1949) Index, the more lines between the species, the greater the association. As er = *Aster ericoides*, Ar lu = *Artemisia ludoviciana*, He gr = *Helianthus grosseserratus*, Po pr = *Poa pratensis*, As tu = *Asclepias tuberosa*, Sp he = *Sporobolus heterolepis*, Zi au = *Zizia aurea*, An gr = *Andropogon gerardi*, So ca = *Solidago canadensis*, Ac la = *Achillea lanulosa*, Ag sm = *Agropyron smithii*.

canadensis in Figure 10F, corresponds generally to the shallower areas of the drainage system. The pattern shown by Figure 10F also includes the species *Apocynum sibiricum, Asclepias incarnata, Carex aquatilis, Carex lasiocarpa, Carex retrorsa, Phalaris arundinacea, Teucrium canadense*, and *Vernonia fasiculata*. The areas covered by these species correspond generally to the Glenco soils as shown in Figure 11. The second, illustrated by *Carex atherodes* and *Scirpus fluviatilis* in Figure 10G and 10H, is more restricted in extent than the above and corresponds to the deeper areas within the drainage system. Species occupying areas equivalent to those shown in Figures 10G and 10H were *Lysimachia hybrida, Polygonum coccineum*, and *Mentha arvensis*. These areas correspond to Glenco-Okoboji and Okoboji soil locations as shown in Figure 11.

In several cases it was noted that two species belonging to the same genus showed opposing patterns of distribution. Examples of this phenomenon are illustrated by the species *Aster laevis* and *Aster simplex*, Figures 10K and 10L; *Helianthus grosseserratus* and *Helianthus laetiflorus*, Figures 10S and 10T; and *Liatris aspera* and *Liatris pycnostachya*, Figures 10U and 10V.

Other species were shown to have patterns corresponding to the distribution of Mima mounds found within the area. Such patterns are shown by *Convolvulus sepium* (Fig. 10F) and by *Oxalis stricta* (Fig. 10Y).

Many factors affect the distribution of a species within the community. It has been shown that individuals of different taxa seldom have identical spatial arrangements within an area (Greig-Smith 1964), yet, as shown above, the distribution patterns of some species may be similar and often show overlapping boundaries. Such species may be closely associated due to preferences for similar microenvironments or, as in the case of *Andropogon gerardi*, because of wide ecological amplitude. Generally these differences in the local distribution of species have been attributed to local microenvironments (i.e., Mima mounds, animal burrows, ridge tops, and drainage ways), interspecific competition (i.e., allelopathy, shade tolerance, etc.), species biology (i.e., modes of reproduction, seed dispersal, immigration rates, etc.), or one to

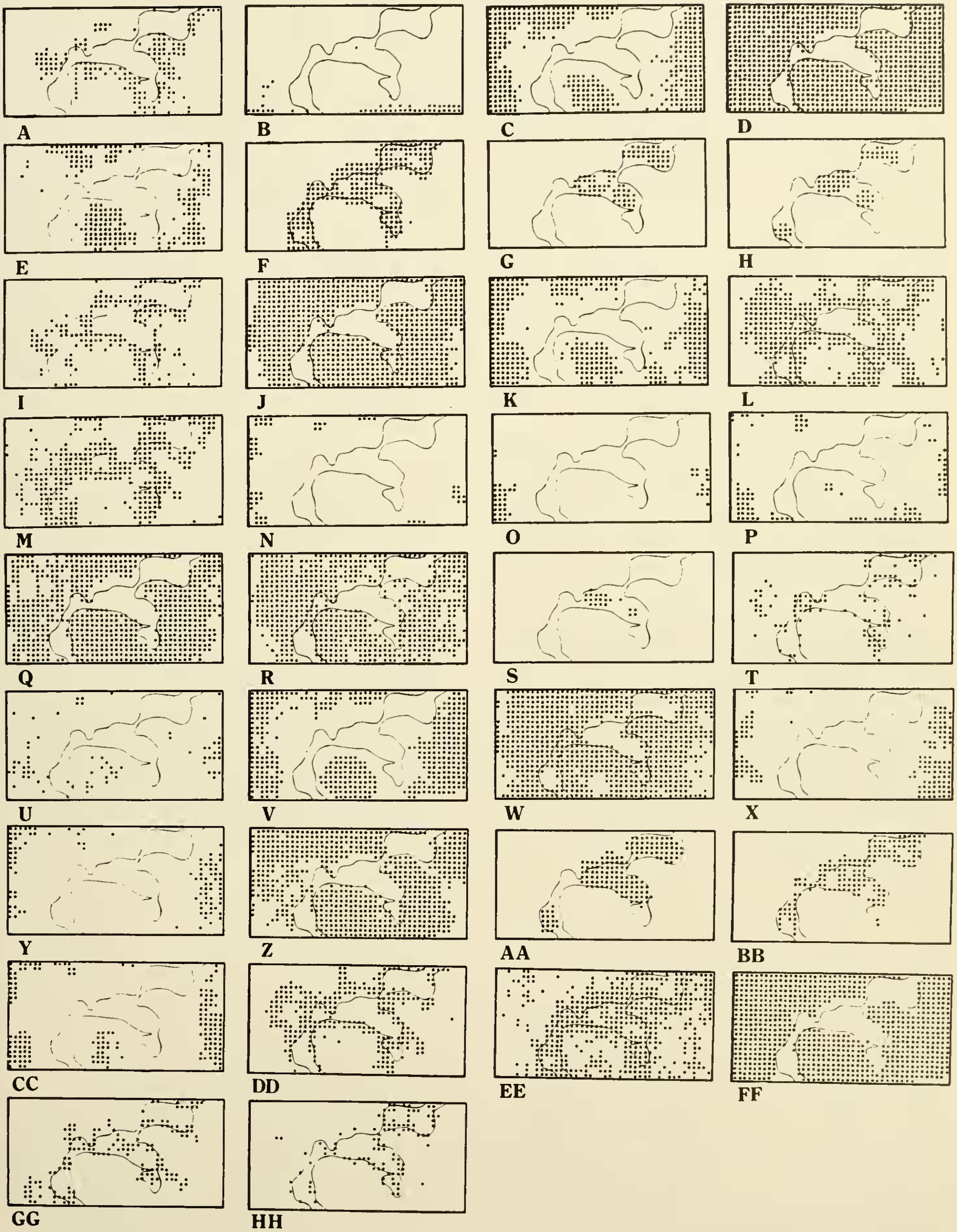

Fig. 10. Distribution patterns in 8 hectare study area of: A. *Agropyron smithii*. B. *Ambrosia artemisifolia*. C. *Amorpha canescens*. D. *Andropogon gerardi*. E. *Solidago nemoralis*. F. *Calamagrostis canadensis*. G. *Carex atherodes*. H. *Scirpus fluviatilis*. I. *Helenium autumnali*. J. *Silphium laciniatum*. K. *Aster laevis*. L. *Aster simplex*. M. *Apocynum sibericum*. N. *Artemisia ludoviciana*. O. *Ceanothus americanus*. P. *Convolvulus sepium*. Q. *Desmodium canadense*. R. *Fragaria virginiana*. S. *Helianthus grosseserratus*. T. *Helianthus laetiflorus*. U. *Liatris aspera*. V. *Liatris pyonostachya*. W. *Lisimachia hybrida*. X. *Lycopus americanus*. Y. *Oxalis stricta*. Z. *Panicum leibergii*. AA. *Polygonum coccineum*. BB. *Phalris arundinacea*. CC. *Psoralea aryophylla*. DD. *Senecio aurens*. EE. *Spartina pectinata*. FF. *Sporobolus heterolepis*. GG. *Teucrium canadense*. HH. *Vernonia fasciculata*.

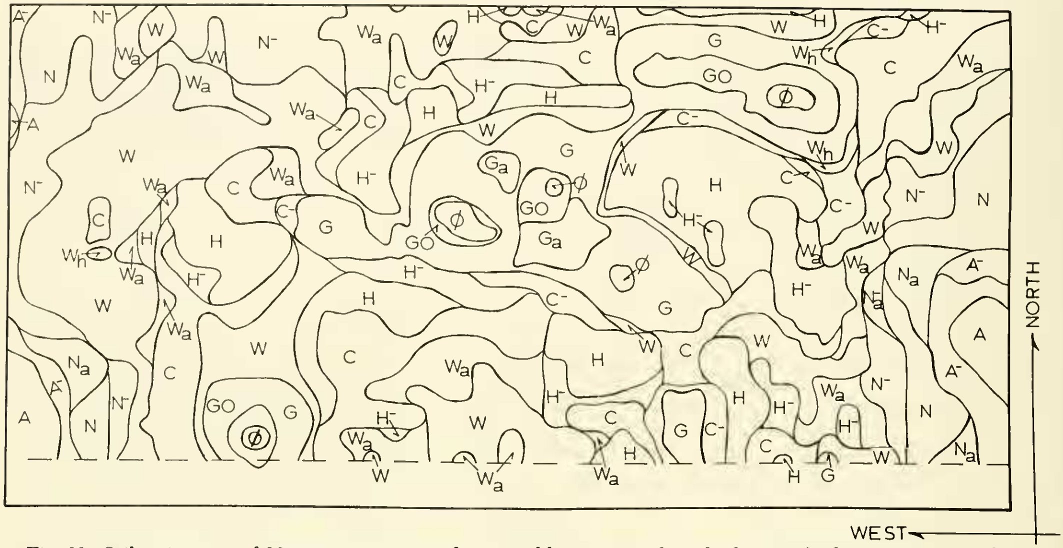

Fig. 11. Soil series map of 20-acre intensive study area, abbreviations described in Methods section. A = Clarion, A⁻ = Clarion-Nicollet, N = Nicollet, Na = calcareous Nicollet, N⁻ = Nicollet-Webster, Na⁻ = calcareous Nicollet-Webster, W = Webster, Wh = heavy Webster, Wa = calcareous Webster, C = Canisteo, H = Harps, H⁻ = Harps-Canisteo, C⁻ = inverted Canisteo-heavy Webster, G = Glenco, Ga = calcareous Glenco, GO = Glenco-Okoboji, O = Okoboji.

several edaphic factors (soil and water regimes, macronutrients, micronutrients, texture, organic matter, etc.) (Curtis 1959, Greig-Smith 1964, Kershaw 1964). From this we can conclude that species showing similar patterns of distribution may be equally well adapted in their response to one or more environmental stimuli and yet differ greatly in their basic ecological amplitudes. The response of individuals to the environmental complex is measured in a species distribution pattern as well as in its importance within the community.

Attempts were made to access the response of the species included in this study to the factors of soil and topography. Soil and elevation readings were recorded at all 968 points of the grid. From these readings a soils map (Figure 11) and contour and elevation maps (Figs. 12, 13) were constructed for the

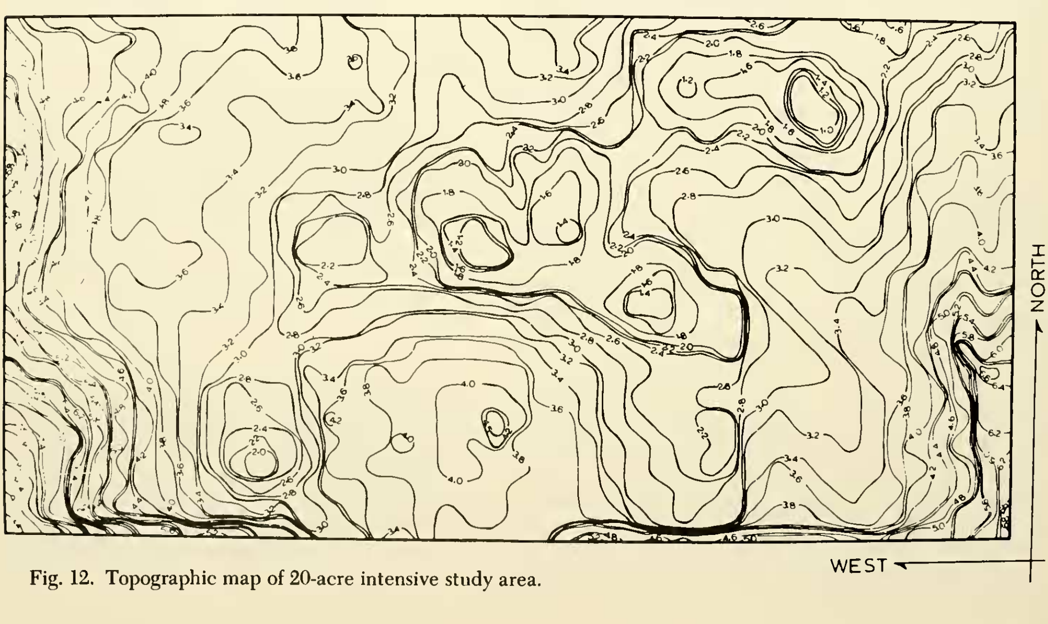

Fig. 12. Topographic map of 20-acre intensive study area.

8 ha plot. This made it possible to group all plant samples according to 0.5 ft changes in elevation or according to soil series. Once grouped, average cover values were computed for all participating species and recorded in Tables 3 (elevation data) and 4 (soils data). As can be seen from these tables, all species showed response to these factors. Several species, *Andropogon gerardi*, *Amorpha canescens*, *Aster ericoides*, *Elymus canadensis*, *Panicum leibergii*, *Poa pratensis*, *Solidago canadensis*, *Sporobolus heterolepis*, and *Zizia aurea*, showed wide tolerance in relation to both soil and elevation, but all exhibited peaks or plateaus of occurrence. These peaks or plateaus are interpreted to represent the optimum conditions under which a particular species can reach its highest importance within the community in relation to the entire species complex.

Other species showed rather narrow ranges of tolerance. Some of these were *Schizachyrium scoparius*, *Apocynum sibiricum*, *Asclepias sullivantii*, *Calamagrostis canadensis*, *Carex atherodes*, *Eryngium yuccifolium*, *Lysimachia hybrida*, *Physalis heterophylla*, *Viola pedatifida* and *Ceanothus americanus*. Those exhibiting narrow ranges also showed peaks of occurrence. For species exhibiting narrow tolerances, four basic types of distribution patterns as related to elevation (Table 3) are recognizable: (1) pothole and drainage, (2) lower slopes, (3) mid- and upper slopes, and (4) ridges.

For species showing response to the soil factor (Table 4) three basic classes are recognizable: (1) Glenco, Glenco-Okoboji, and Okoboji, (2) calcareous, and (3) noncalcareous and ridge. Species indicating preference for class 1 were *Calamagrostis canadensis*, *Carex atherodes*, *Carex aquatilis*, *Carex lasiocarpa*, *Carex retrorsa*, *Lysimachia hybrida*, *Polygonum coccineum*, and *Scirpus fluviatilis*. Species showing preference for the calcareous soils (class 2) were *Agropyron smithii*, *Desmodium canadense*, *Galium obtusum*, *Helenium autumnale*, *Petalostemum purpureum*, *Senecio pauperculus*, *Silphium laciniatum*, *Solidago canadensis*, *Solidago nemoralis* and *Solidago riddellii*. Examples of species preferring class 3 were *Amorpha canescens*, *Artemisia ludoviciana*, *Asclepias tuberosa*, *Baptisia leucophaea*, *Eryngium yuccifolium*, *Lathyrus palustris*, *Panicum leibergii*, *Poa pratensis*, *Solidago missouriensis*, *Vicia americana*, and *Ceanothus americanus*.

These groups of recognizable patterns, each involving several species, suggest the existence of subcommunities within the prairie area. To ascertain the existence of such communities, the data from Tables 3 and 4 were treated using Orloci's (1966) method of ordination. When the results from the soils analysis were plotted (Fig. 14), four basic groups

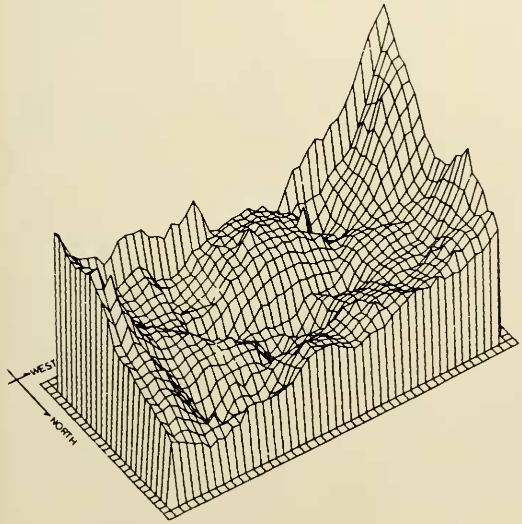

Fig. 13. Topographic map of 20-acre intensive study area plotted by computer.

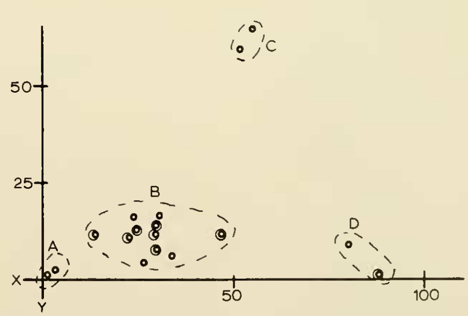

Fig. 14. Two-dimensional ordination of vegetation found on the different soil types in the 20-acre study area; cluster A indicates vegetation on Nicollet and Nicollet-Webster soil types; B indicates vegetation on Clarion, Clarion-Nicollet, Webster, heavy Webster, calcareous Nicollet, calcareous Nicollet-Webster, calcareous Webster, Canisteo, Harps, Harps-Canisteo, and inverted Canisteo-heavy Webster soil types; C indicates vegetation on Glenco-Okoboji and Okoboji soil types; D indicates vegetation on Glenco and calcareous Glenco.

TABLE 3. Average cover values for species in relation to elevation in 20-acre intensive study area.

Species	1 .7–1.2	2 1.3–1.8	3 1.9–2.4	4 2.5–3.0	5 3.1–3.6	6 3.7–4.2
Achillea lanulosa				.23	.23	.28
Agropyron smithii			.02	.12	.09	
Ambrosia artemisifolia				.01	.01	.55
Amorpha canescens				.20	1.49	4.27
Andropogon gerardi		.52	5.57	9.06	9.49	10.10
Schizachyrium scoparius			.25	.92	.75	.55
Anemone canadensis					.02	.03
Anemone cylindrica						
Apocynum sibiricum	1.36	1.98	1.15	.65	.04	.19
Arabis hirsuta					.01	
Artemisia ludoviciana					.06	.02
Asclepias incarnata		.52				
Asclepias sullivantii				.08	.02	
Asclepias syriaca			.13		.07	.28
Asclepias tuberosa			.02	.02	.44	.71
Aster ericoides			.41	1.87	2.09	1.72
Aster laevis				.10	.77	1.84
Aster simplex		.56	2.72	2.55	1.66	.82
Baptisia leucantha						
Baptisia leucophaea					.13	
Calamagrostis canadensis	1.59	33.65	36.13	9.52	1.09	
Carex atherodes	34.55	16.35	4.28	.23		
Carex aquatilis		2.05	3.22	1.33	.19	.02
Carex gravida					.01	
Carex lasiocarpa		1.63	1.91	.53	.08	
Carex retrorsa		4.51	7.24	2.67	.57	.02
Chenopodium album			.02		.14	
Cicuta maculata						
Cirsium altissimum			.54	.55	.67	.44
Comandra umbellata		.03	.02	.14	.38	.32
Convolvulus sepium					.09	.03
Desmodium canadense			.72	2.37	3.49	2.96
Elymus canadensis			.11	.49	1.05	.85
Equisetum kansanum			.04	.14	.21	.24
Eryngium yuccifolium					.05	.91
Fragaria virginiana			.89	.92	1.91	1.11
Galium obtusum		.90	1.91	1.69	1.84	.93
Gentiana andrewsii		.21		.01	.06	.13
Helenium autumnale		.03	.28	.19	.18	.02
Helianthus grosseserratus		2.95	8.89	8.88	7.46	4.59
Helianthus laetiflorus				.01	.43	1.39
Helianthus maximiliani					.01	
Heliopsis helianthoides				.28	.22	.24
Lactuca scariola				.02	.06	.03
Lathyrus palustris		.03	.02	.08	.06	
Lathyrus venosus						.06
Lespedeza capitata				.01	.01	.11
Liatris pycnostachya			.20	.80	.63	.65
Lithospermum canescens			.07	.26	.34	.33
Lycopus americanus			.24	.13		.03
Lysimachia chiliata					.01	
Lysimachia hybrida		21.50	1.42			
Lysimachia quadriflora			.07	.04	.03	.03
Lythrum alatum		.24	.20	.12		
Mentha arvensis		.28		.08		
Muhlenbergia racemosa			.52	.78	.25	.22
Oxalis stricta				.18		
Panicum capillare					.01	

Table 3 continued.

7	8	9	10	11	12	13	14	15
4.3–4.8	4.9–5.4	5.5–6.0	6.1–6.6	6.7–7.2	7.3–7.8	7.9–8.4	8.5–9.0	9.1–9.6
.71	1.00	1.07	.13			8.00		
.05		.71						
2.03	4.50	1.79	1.71	7.86	.83	7.50	1.25	
11.70	14.67	10.95	26.21	14.29	57.92	40.00	20.00	
1.42								
.33	.08	.71	2.50	4.29		3.00		
		.71						
1.46	.25	.71						
3.35	3.08	2.02	7.89	2.50		3.50	1.25	
1.37	2.42	4.76	7.37	2.50	5.83	1.00		
.09								
.28								
.33	1.08							
		.12						
.33				2.14				
.24		.12						
			.79	2.14	2.92	3.00	7.50	
2.36	2.08	2.50	.26	2.14				
.71	.25	.48	.26	.71	.42		1.25	
.09	.08			.36		.50		
.09	.08	.71						
.99	.08		.13					
.52	.25	.12	.13	.71				
3.82	.83	.24						
3.16	2.67	2.50	8.16	5.71				
.14			.79					
.33	.17	.12	.39					
.28	.08							
.24	.08							
.47	.25	.24	.53		.42			
	.50	.71						
.05		.71						
.05								

Table 3 continued.

Species	1 .7–1.2	2 1.3–1.8	3 1.9–2.4	4 2.5–3.0	5 3.1–3.6	6 3.7–4.2
Panicum leibergii			.02	.51	1.19	2.31
Panicum virgatum			.26	.66	.86	.60
Pedicularis canadensis				.47	.09	.13
Petalostemum candidum			.02		.02	.02
Petalostemum purpureum		.03	.13	.59	.40	.35
Phalaris arundinacea	7.05	5.49	3.98	.49		
Phlox pilosa			.04	.05	.13	.13
Physalis heterophylla						
Physalis virginiana				.01	.04	.03
Poa pratensis			1.24	2.82	3.57	4.24
Polygonum coccineum	27.27	16.81	4.02	1.52	.01	
Potentilla arguta						.02
Psoralea argophylla					.02	.09
Pycnanthemum virginianum			.37	1.83	.77	.35
Ratibida pinnata		.21	.30	1.65	1.93	1.50
Rosa suffulta				.24	.46	.91
Rudbeckia hirta			.10		.01	.03
Scirpus atrovirens		.52				
Scirpus fluviatilis	2.05	6.22	1.41	.08		
Scutellaria leonardii			.07	.04	.13	.08
Senecio pauperculus		.42	3.15	3.92	.59	.35
Setaria lutescens			.13		.01	.09
Setaria viridis				.01	.03	.24
Silphium laciniatum			2.09	4.84	2.75	2.10
Solidago canadensis		.66	3.98	6.02	5.68	2.12
Solidago gymnospermoides				.01	.31	.11
Solidago missouriensis				.01		.09
Solidago rigida				1.81	3.20	5.44
Sorghastrum nutans			.09	.17	.42	.08
Spartina pectinata	1.36	4.27	3.74	1.79	.84	.30
Sporobolus heterolepis		.52	7.76	23.83	40.98	49.78
Stipa spartea						.05
Teucrium canadense		.03	1.07	.31	.01	
Thalictrum dasycarpum				.04	.44	.33
Vernonia fasiculata			.59			
Veronicastrum virginicum						.02
Viola pedatifida					.04	.08
Viola sp.			.07	.12	.12	.08
Vicia americana					.05	.05
Zizia aurea		.21	1.43	3.28	4.18	2.74
Allium sp.					.02	
Aster novae-angliae				.23	.02	
Cacalia tuberosa						.02
Ceanothus americana					.01	
Panicum implicatum					.06	.09
Prenanthes racemosa				.08		
Solidago nemoralis			.02	.13	.45	1.69
Solidago riddellii		.03	.13	.69	.18	.03
Taraxacum officinale						.09
Echinacea pallida						.02

were recognizable. These groups are labeled A, B, C, and D, with group A corresponding to the noncalcareous and ridge entity described previously and made up of plants showing preference for Nicollet and Nicollet-Webster soils. Group B includes all but one of the calcareous soil types plus four noncalcareous types. The noncalcareous types are found at the periphery of the group and include Clarion, Clarion-Nicollet, Webster, and heavy Webster soil types. Group C includes the Glenco-Okoboji and Okoboji soils, and group D includes Glenco and calcareous-Glenco soils. These last two groups correspond to class 1 for species showing response to the soil factor described above.

Table 3 continued.

7	8	9	10	11	12	13	14	15
4.3–4.8	4.9–5.4	5.5–6.0	6.1–6.6	6.7–7.2	7.3–7.8	7.9–8.4	8.5–9.0	9.1–9.6
2.64	2.16	2.62	9.74	2.50	2.92	.50		
.24	.67		.13					
	.17		.13					
.09	.58							
		.12						
			4.87	2.14	5.00			
.09		.12	.13		2.50			
7.36	9.25	26.55	22.50	27.86	26.67	38.50	61.25	
		.71	.13					
.05	1.00	.83	.13	.71	2.92	.50		
.24	.17							
1.46	2.75		2.11					
2.03	1.50	2.62	1.18				1.25	
.09				.36				
.57								
		2.50	.79					
2.41		4.88	.13					
.61								
2.22	3.50	2.38	4.34	11.43	2.92		7.50	
			1.58		2.50			
5.66	3.17	2.74	.79					
.09			.26					
.05								
42.74	43.08	26.90	17.63	33.21	8.75	8.00		
.09	.08	.95	.26			.50	1.25	
			.13					
.42								
.09	.08							
.05								
.09			.26		.42			
2.36	.25	1.31	.13		.42			
	.50		1.97	2.14	2.50	24.50		
.05								
.05								

Ordination of elevation data (Fig. 15) showed no recognizable groupings. Instead it separated the different elevation classes (Table 3) along a curve, point 14 representing the ridge tops and point 1 representing the bottom of the potholes. This would tend to support statements made earlier that the vegetation of Kalsow Prairie is best represented by the continuum concept of Curtis and McIntosh (1951).

The definable subcommunities or groups (Fig. 14) as based on soils data represent the response of the different taxa in the vegetation to an environmental stimulus (i.e., carbonate soils) that is not distributed along gradients (i.e., at 9 × 9 m sampling levels)

TABLE 4. Average cover values for species in relation to soil series in 20-acre intensive study area.

Species	A	A^-	N	Na	N^-	Na^-	W
Achillea lanulosa	.14	.19	.57		.44	.21	.37
Agropyron smithii							.01
Ambrosia artemisifolia		.56					
Amorpha canescens	3.47	2.87	4.16	4.06	6.57		2.56
Andropogon gerardi	39.72	19.25	12.26	21.56	10.04	10.63	6.70
Schizachyrium scoparius					.08		.80
Anemone canadensis							.03
Apocynum sibiricum							.09
Arabis hirsuta							
Artemisia ludoviciana	3.19	.56	.38	1.88	.12		
Asclepias incarnata							
Asclepias sullivantii							
Asclepias syriaca			.28				.01
Asclepias tuberosa		.65	.61	1.88	.73		.19
Aster ericoides	3.89	1.94	3.58	2.19		.42	1.50
Aster laevis	3.47	4.44	1.56	9.68	1.29	2.50	.46
Aster simplex					.08		2.12
Baptisia leucophaea	.14		.85	1.88	.24		.03
Calamagrostis canadensis							10.48
Carex atherodes							.75
Carex aquatilis							1.11
Carex gravida							.01
Carex lasiocarpa							.28
Carex retrorsa							2.07
Chenopodium album							.01
Cirsium altissimum			.33		.48		.60
Comandra umbellata	.14	.19	.19		.08	.21	.05
Convolvulus sepium	.97		.28		.04		
Desmodium canadense		.65	1.88	2.19		2.71	1.64
Elymus canadensis	.28	.19	.24	2.19	.44	1.04	.60
Equisetum kansanum	.14		.05	.31	.44	.42	.12
Eryngium yuccifolium			.61		.65		.38
Fragaria virginiana	.14	.19	.24		.16		2.15
Galium obtusum			.14		.65	.42	1.83
Gentiana andrewsii							.01
Helenium autumnale							.03
Helianthus grosseserratus			1.65	.31	2.58	1.25	9.26
Helianthus laetiflorus	3.19	6.20	3.87	6.87	2.18	4.79	.18
Helianthus maximiliani							
Heliopsis helianthoides			.28				.03
Lactuca scariola					.24		.01
Lathyrus palustris							.08
Lathyrus venosus	.56	.09	.24	1.88			
Lespedeza capitata		.65				.21	
Liatris pycnostachya			.14	.31	1.21		.40
Lithospermum canescens	.28	.56	.52	.31	.56	1.04	.17
Lycopus americanus					.04		.11
Lysimachia chiliata							
Lysimachia hybrida							
Lysimachia quadriflora							.03
Lythrum alatum							.01
Mentha arvensis							.12
Muhlenbergia racemosa						.21	.23
Oxalis stricta		.09		1.88			
Panicum capillare						.21	.01
Panicum leibergii	6.67	7.50	2.64	4.06	.77	3.33	1.20
Panicum virgatum		1.20	.14		.44	2.71	.49
Pedicularis canadensis					.04		
Petalostemum candidum		.19	.09				
Petalostemum purpureum		.65			.12		.21

Table 4 continued.

Wh	Wa	C	H	H⁻	C⁻	G	Ga	GO	O
.42	.40	.07	.02	.09	.65				
.10		.09	.22	.17					
					.09				
.73	1.93	.33	.33	.04		.02			
12.19	9.09	10.87	14.42	11.57	14.25	.05	.13		
.63	.77	.46	1.74	1.31		.02			
			.02						
.73		.09	.25		.74	2.06	3.50	2.63	
			.02						
	.17								
								1.88	
	.03	.02	.16						
		.18							
	.71	.64	.07	.81					
2.81	1.22	2.81	2.59	2.42	1.76				
	1.70	1.18	.31	.55					
3.54	1.02	1.36	1.63	1.18	3.98	1.80	2.38		
	.17								
11.15		2.46	1.41	.81	13.61	45.26	56.88	1.50	
.63				.25		7.73	8.25	32.38	21.50
1.88		.20	.11	.64	1.48	3.90	3.00		
1.04		.04	.16	.25	.39	2.48	3.88	.25	
6.88		.37	.58	1.23	1.38	8.27	10.63	6.00	
.10	.77	.50	.67	.68	.19	.35			
	.45	.64	.16	.30	.09				
.10	.48					.14			
1.35	4.66	3.53	2.79	4.15	2.69	.14			
.31	1.08	1.10	.56	1.10	.37	.07			
.10	.31	.15	.11	.17					
	.26	.02							
.52	2.24	1.62	.96	.98	1.57	.07	.13		
2.08	1.42	2.43	1.52	2.16	1.85		.13		
		.18				.14			
		.31	.58	.30	.09				
13.85	5.17	9.96	7.86	6.31	12.41	3.36	4.63		
.10	.20			.04					
			.02						
	.34	.31	.18	.34	.65				
	.06		.02						
.10	.06		.05	.09		.02			
.10									
	.23								
.63	1.02	.72	.67	.42	.28				
.10	.48	.33	.22	.21	.09				
.10	.03	.02	.18	.04	.09	.05	.13		
		.02							
						.28			17.25
	.03	.02	.11	.04	.09				
						.19	.25		
						.02	1.31		
.10	.20	.42	1.47		.93	.05	.75		
	.43								
	2.70	1.57	.05	.68					
.31	.80	1.03	.51	.30	.83				
	.20	.46	.45	.25					
	.06		.02						
.31	.60	.50	.87	.42	.28				

TABLE 4. Average cover values for species in relation to soil series in 20-acre intensive study area.

Species	A	A⁻	N	Na	N⁻	Na⁻	W
Phalaris arundinacea							1.09
Phlox pilosa		.19			.16		.03
Physalis heterophylla		2.31	.28	1.88			
Physalis virginiana	.14	.09	.28		.08		.03
Poa pratensis	16.53	31.09	5.99	32.81		5.21	3.22
Polygonum coccineum							.44
Potentilla arguta	.14	.56	.05				
Psoralea argophylla	1.81	1.30	.15	.31	.08	.21	
Pycnanthemum virginianum		.28					.43
Ratibida pinnata	2.92	3.24	.05		.32	1.46	1.29
Rosa suffulta	.14	3.06	1.56	2.19		1.67	.29
Rudbeckia hirta					.04		
Scirpus atrovirens							
Scirpus fluviatilis							.01
Scutellaria leonardii		.09	.05		.08		.14
Senecio pauperculus							1.24
Setaria lutescens		.56					
Setaria viridis		.56		.31			
Silphium laciniatum			.38			1.25	2.15
Solidago canadensis	.14	2.41	3.21	.31	2.86	1.25	3.16
Solidago gymnospermoides			.09		.69	1.88	
Solidago missouriensis	1.67	.56	.28				
Solidago rigida		.56	3.25	.31	4.27	2.50	3.79
Sorghastrum nutans				.31	.20		.11
Spartina pectinata					.04		.83
Sporobolus heterolepis	12.08	21.76	62.69	37.19	58.95	27.92	37.41
Stipa spartea	.97	.09	.14		.08	.21	.05
Teucrium canadense			.05			.21	.23
Tahlictrum dasycarpum							.05
Vernonia fasciculata							.09
Veronicastrum virginicum							.01
Viola pedatifida			.09		.12		.05
Viola sp.							.03
Vicia americana	.28	.09	.05	.31	.04		.03
Zizia aurea	.14	.93	4.58	4.06	1.73	3.33	1.52
Allium sp.							
Aster novae-angliae							.09
Cacalia tuberosa							.01
Ceanothus americana	10.56	.56			.04		
Panicum implicatum					.04		.15
Prenanthes racemosa							.09
Solidago nemoralis			.28		.93		.75
Solidago riddellii							.01
Taraxacum officinale							

but in mappable units with fairly discrete boundaries. This would tend to cause vegetation sensitive to carbonate influence to group accordingly.

An ordination of species, utilizing the data from Tables 3 and 4, isolated taxa having distinct distribution patterns. These species are *Amorpha canescens, Andropogon gerardi, Aster ericoides, Aster laevis, Calamagrostis canadensis, Carex athorodes, Carex aquatilis, Desmodium canadense, Helianthus grosseserratus, Helianthus laetiflorus, Panicum leibergii, Phalaris arundinacea, Poa pratensis, Polygonum coccineum, Ratibida pinnata, Scirpus fluviatilis, Silphium laciniatum, Solidago canadensis, Solidago rigida, Spartina pectinata, Sporobolus heterolepis, Zizia aurea,* and *Ceanothus americanus,* all of which show distinct distribution patterns and in many cases high preference for certain soil groups or elevations.

The relationships between elevation and soil series are shown in Figure 16. The soil types are positioned along the base line as

Table 4 continued.

Wh	Wa	C	H	H^-	C^-	G	Ga	GO	O
1.56						6.24	6.63	.75	
.63	.20	.09	.07	.17	.09				
	.06	.02	.05						
1.35	2.81	3.86	3.15	3.18	5.74	.05			
				.25		8.74	2.88	40.50	36.75
.10	.06								
.10	.45	.99	2.17	1.99	.83				
.10	1.73	3.05	1.94	1.91	.09				
	.68	.42	.20	.25					
		.09	.16						
						.35			
						1.87		13.63	17.50
.21	.11	.04	.09	.09	.09				
3.65	.48	2.45	3.59	2.84	9.17		.13		
						.14			
				.25					
7.40	2.95	3.84	4.69	4.79	3.61	.28	.75		
2.50	4.12	7.30	7.39	5.30	13.43	.05			
	.26			.09					
			.05						
.63	5.34	3.77	1.36		1.20				
.10	.17	.35	.63	.34	.09				
1.88	.28	.15	.54	.85	.56	7.22	6.88	3.38	
29.38	44.40	25.42	24.08	32.80	9.44	.79	.13		
.73	.28	.15	.38	.25	.09	.30		.13	
		.20	.38	.17	.09				
						.49			
.21				.04					
	.09	.31	.09	.25	.09				
	.09	.02	.02						
.31	3.41	5.31	4.64	5.13	3.52				
.10			.02						
		.13	.05	.04	.56				
		.04							
.73	1.02	.31	.47	.17					
2.92	.09	.50	.45	.03	.19				

they appeared in the field. In all cases where the noncalcareous soils had adjacent calcareous variants the calcareous variants showed higher average elevations.

Summary and Conclusions

1. *Sporobolus heterolepis* is the dominant plant of the upland prairie that places Kalsow Prairie within the "Consociation" designated by Weaver and Fitzpatrick (1934) as the Prairie-Dropseed type.

2. The vegetation of the upland prairie communities is best described and represented by the continuum concept as described by Curtis (1955).

3. The vegetation of the upland prairie has changed since Moyer's 1953 study. Species showing increased importance in my study are *Solidago canadensis, Solidago rigida, Panicum leibergii, Helianthus grosseserratus,* and *Fragaria virginiana.* Species decreasing in importance were *Phleum pratense, Poa pratensis, Zizia aurea, Schizachyrium scoparius,*

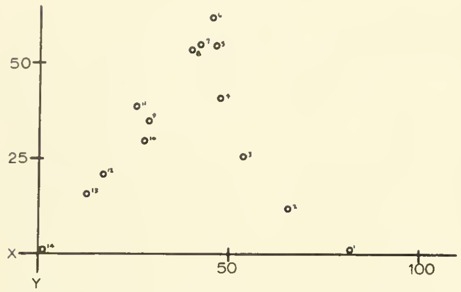

Fig. 15. Two-dimensional ordination of vegetation found at different elevations in the 20-acre study area; 1 = .7–1.2 feet elevation, 2 = 1.3–1.8 feet elevation, 3 = 1.9–2.4 feet elevation, 4 = 2.5–3.0 feet elevation, 5 = 3.1–3.6 feet elevation, 6 = 3.7–4.2 feet elevation, 7 = 4.3–4.8 feet elevation, 8 = 4.9–5.4 feet elevation, 9 = 5.5–6.0 feet elevation, 10 = 6.1–6.6 feet elevation, 11 = 6.7–7.2 feet elevation, 12 = 7.3–7.8 feet elevation, 13 = 7.9–8.4 feet elevation, 14 = 8.5–9.0 feet elevation.

Panicum virgatum, Sorghastrum nutans, and *Sporobolus heterolepis*.

4. Soil series, elevations, and species distribution patterns were mapped on an 8 ha intensive study plot. Elevation and soils data are correlated with species distribution patterns. All species show a response. Nine general patterns of distribution are described, with the following species as examples:

a. *Andropogon gerardi*—species of wide distribution, limited only by conditions peculiar to the drainage areas of the prairie.
b. *Silphium laciniatum*—a pattern closely resembling that of *Andropogon gerardi* but showing limited distribution on the higher and drier ridges.
c. *Ambrosia artemisifolia*—species limited to the border weed communities.
d. *Amorpha canescens*—a pattern common to species limited to the ridges and lower slopes.
e. *Solidago nemoralis*—species limited to mid- and upland slopes of the prairie.
f. *Ceanothus americanus*—a pattern limited to the ridges and drier sites of the prairie.
g. *Helenium autumnale*—limited to growth on soils that are highly calcareous to the surface.
h. *Calamagrostis canadensis*—limited to growth along the shallower areas of the pothole and drainage system.
i. *Scirpus fluviatilis*—growth corresponds to deeper areas within the drainage system.

5. Species occurring in the intensive study were ordinated using Orloci's (1966) method. The technique did not delineate associated groups of species, yet it pointed out species exhibiting peculiar distribution patterns. Such species are useful as indicator species.

6. Indices of interspecific association were computed for all participating species (Cole 1949) and found to be extremely useful in identifying clusters or groups of species having similar ecological amplitudes.

Literature Cited

Aikman, J. M. 1959. Prairie research in Iowa. The American Biology Teacher 21:7–8.

Aikman, J. M., and R. F. Thorne. 1956. The Cayler Prairie: an ecologic and taxonomic study of a northwest Iowa prairie. Iowa Acad. Sci. 63:177–200.

Brennan, K. M. 1969. Vertebrate fauna of Kalsow Prairie. Unpublished thesis. Iowa State Univ.

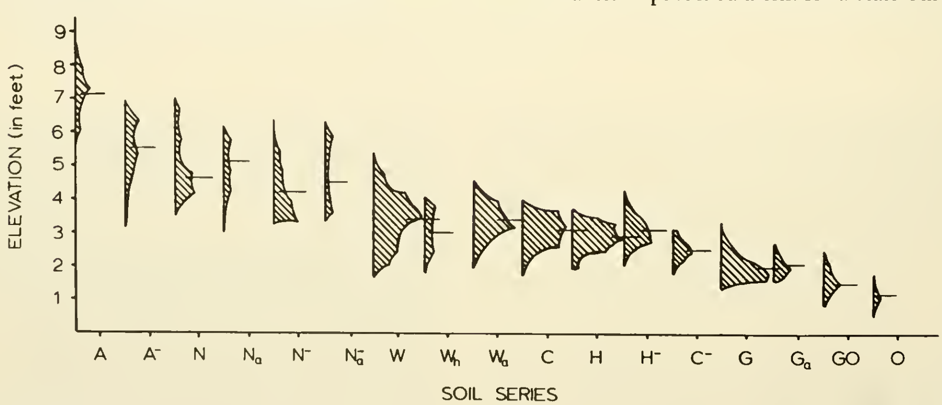

Fig. 16. Relationships between elevation and soil series as found in 20-acre intensive study area; mean value indicated for each soil by short horizontal line.

CAIN, S. A., AND F. C. EVANS. 1952. The distribution patterns of three plant species in an old-field community in southeastern Michigan. Contributions from the Laboratory of Vertebrate Biology No. 52.

COLE, L. C. 1949. The measurement of interspecific association. Ecology 30:411–424.

COLLINS, G. B. 1968. Implications of diatom succession in postglacial sediments from two sites in northern Iowa. Unpublished dissertation. Iowa State Univ.

CRAWFORD, R. M. M., AND D. WISHART. 1968. A rapid classification and ordination method and its application to vegetation mapping. Ecology 56:385–404.

CURTIS, J. T. 1955. A prairie continuum in Wisconsin. Ecology 36:558–566.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–66.

DICK-PEDDIE, W. A. 1955. Presettlement forest types in Iowa. Unpublished thesis. Iowa State Univ.

DIX, R. L., AND J. E. BUTLER. 1960. A phytosociological study of a small prairie in Wisconsin. Ecology 41:316–327.

EHRENREICH, J. H. 1957. Management practices for maintenance of native prairies in Iowa. Unpublished dissertation. Iowa State Univ.

ESAU, K. L. 1968. Carabidae (Coleoptera) and other arthropods collected in pitfall traps in Iowa cornfields, fencerows, and prairies. Unpublished dissertation. Iowa State Univ.

GILLY, C. L. 1946. The Cyperaceae of Iowa. Iowa State Coll. J. Sci. 21:55–151.

GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Lancaster Press, Lancaster, Pennsylvania. 3 vols.

GREIG-SMITH, P. 1964. Quantitative plant ecology. Butterworth. Washington, D.C.

HALE, M. E., JR. 1955. Phytosociology of corticolous cryptograms in the upland forests of southern Wisconsin. Ecology 36:45–62.

HAYDEN, ADA. 1943. A botanical survey in the Iowa lake region of Clay and Palo Alto counties. Iowa State Coll. J. Sci. 17:277–416.

———. 1945. The selection of prairie areas in Iowa which should be preserved. Proc. Iowa Acad. Sci. 52:127–148.

———. 1946. A progress report on the preservation of prairie. Proc. Iowa Acad. of Sci. 53:45–82.

HEWES, L. 1950. Some features of early woodland and prairie settlement in a central Iowa county. Annals Assoc. Amer. Geog. 40:40–57.

HURLBERT, S. H. 1969. A coefficient of interspecific association. Ecology 50:1–9.

KENNEDY, R. K. 1969. An analysis of tall-grass prairie vegetation relative to slope position, Sheeder Prairie, Iowa. Unpublished thesis. Iowa State Univ.

KERSHAW, K. A. 1964. Quantitative and dynamic ecology. Edward Arnold, Ltd., London, England.

LANDERS, R. Q. 1966. Visit the virgin prairie. Iowa Farm Science 21:418–419.

MOYER, JOHN F. 1953. Ecology of native prairie in Iowa. Unpublished dissertation. Iowa State Univ.

NORTON, D. C., AND P. E. PONCHILLIA. 1968. Stylet-bearing nematodes associated with plants in Iowa prairies. J. Iowa Acad. Sci. 75:32–35.

ORLOCI, L. 1966. Geometric models in ecology. I. The theory and application of some ordination methods. J. Ecology 54:193–215.

OSCHWALD, W. R. ET AL. 1965. PRINCIPAL SOILS OF IOWA. SPECIAL REPORT NO. 42, DEPARTMENT OF AGRONOMY, IOWA STATE UNIV.

POHL, R. W. 1966. The grasses of Iowa. Iowa. Iowa State J. Sci. 40:341–566.

RICHARDS, M. S. 1966. Observations on responses of prairie vegetation to an April fire in central Iowa. Unpublished thesis. Iowa State Univ.

RUHE, R. V. 1969. Quaternary landscapes in Iowa. Iowa State Univ. Press, Ames Iowa. 249 pp.

RYDBERG, P. A. 1931. A short phytogeography of the prairies and great plains of central North America. Brittonia 1:57–66.

SANDERS, D. R. 1969. Structure and pattern of the herbaceous understory of deciduous forests in central Iowa. Unpublished dissertation. Iowa State Univ.

SCHMITT, D. P. 1969. Plant parasitic nematodes and nematode populations in the Kalsow Prairie. Unpublished thesis. Iowa State Univ.

SHIMEK, B. 1911. The prairies. Bull. Lab. Nat. Hist., State Univ. Iowa 6:169–240.

SHIMEK, B. 1915. The plant geography of the Lake Okoboji region. Bull. Lab. Nat. Hist., State Univ. Iowa 7:1–90.

SHIMEK, B. 1925. The persistence of the prairie. Univ. of Iowa Studies 11:3–24.

STEIGER, T. L. 1930. Structure of prairie vegetation. Ecology 11:170–217.

U.S. GOVERNMENT. 1868. First survey of the State of Iowa. Plats deposited in the State House, Des Moines.

WEAVER, J. E. 1930. Underground plant development in its relation to grazing. Ecology 11:543–557.

WEAVER, J. E. 1954. North American prairie. Lincoln, Nebraska, Johnsen Publishing Company. 348 pp.

WEAVER, J. E., AND F. E. CLEMENTS. 1938. Plant Ecology. 2d ed. McGraw-Hill, New York.

WEAVER, J. E., AND T. J. FITZPATRICK. 1932. Ecology and relative importance of the dominants of the tallgrass prairie. Bot. Gaz. 93:113–50.

WEAVER, J. E., AND T. J. FITZPATRICK. 1934. The prairie. Ecol. Monogr. 4:109–295.